Settlement and recruitment processes in the southern rock lobster, *Jasus edwardsii*:

The influence of oceanographic features, pueruli behaviour and kelp habitat

by

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STATEMENTS AND DECLARATIONS

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GENERAL ABSTRACT

Settlement processes and subsequent post-settlement survival influence the demographic structure of marine populations and also their resilience to human exploitation, or other perturbations. Therefore, better understanding of these two periods of the lifecycle could assist in the management and conservation of economically important species. The rock lobster, *Jasus edwardsii*, supports valuable fisheries throughout southern Australia and New Zealand. Settlement levels of pueruli (late larval-stage) have been monitored on artificial crevice collectors throughout the geographical range with a long-term program that commenced in the early 1990's. Examination of the settlement patterns indicated that most areas of the Australian fishery suffered declines in settlement at some time between 2000 and 2010. Patterns in settlement at some sites appear to be partially driven by environmental processes that move pueruli inshore by onshore advection. However, a lack of correlation with environmental variables at other sites, and the strong swimming ability of the pueruli, suggested that the process of settlement inshore is complex and is influenced by the ability of pueruli to orientate onshore, although no behavioural experiments demonstrating this have been reported for *J. edwardsii*. Settlement behaviour is also of interest in the Tasmanian jurisdiction because climate-change has led to the loss of giant kelp (*Macrocystis pyrifera*) forests, which previously provided dense cover across large areas of the east coast. This change in habitat in areas important to the fishery has also raised the question of whether there were effects on puerulus settlement and post-settlement survival.

This thesis used a combination of data analyses, and laboratory and field experiments to assess the influence of environmental variables and puerulus behaviour on settlement and post-settlement survival. To assess the contribution of environmental variables on settlement magnitude, time series analyses were conducted over different spatial scales (Chapter 2). In addition, laboratory and field experiments were conducted to examine whether the pueruli used

chemical cues from coastal waters and from the giant kelp (Chapter 3), and underwater reef noise (Chapter 4) for orientation to find settlement habitat. The effect of kelp forest depletion on settlement and survival of pueruli and early juveniles was examined with field experiments (Chapter 5). Settlement was found to be affected by regional scale oceanic processes (100-500's km) measured by the Southern Oscillation Index (SOI), Dipole Mode Index (DMI) and Southern Hemisphere Annular Mode (SAM) although outcomes varied between regions. At a local scale, waves, wind strength and current appeared to have some influence on pueruli transport, with sea surface temperatures being less important, but much of the settlement variability was not explained and the effect of environmental factors was not consistent between sites. In a field experiment it was found that underwater reef noise was detected by puerulus and appeared to be an attractant for settlement during calm sea conditions. Laboratory experiments showed that pueruli were attracted to chemical cues from coastal waters, but they were not attracted to chemical cues from the giant kelp. The effect of kelp was also examined in field experiments where kelp habitats increased settlement into crevice collectors and the subsequent survival of the early juveniles, indicating that decline in kelp habitat could reduce recruitment at a local scale. Overall, these results highlight the complexity of settlement and recruitment where larval behaviour and oceanographic process interact at different scales. The research helps to explain settlement processes and also has value for including puerulus behaviour into future dispersal models for exploring spatial patterns and testing dispersal hypotheses in this species which supports a valuable fishery. The apparently complex processes affecting settlement strength showed that environmental conditions that reduce settlement strength in one region of the fishery often increase settlement strength in other regions. This suggests resilience to climate change at the scale of the entire fishery. However, local habitat changes would also be expected to affect future recruitment of this valuable species.

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Chapter 1: General Introduction

"Science and management demands that complex systems be simplified, but the art of appropriate simplification depends on a basic understanding of the important natural history" Paul K. Dayton (2003).

One of the major drivers of the population dynamics of marine organisms is the variability in supply of settlers or recruits (Underwood and Fairweather, 1989). Most marine species include a larval stage in their life cycle which is the means for the population to replenish and disperse (Keough and Swearer, 2007). The pelagic larvae of benthic species from shallow coastal waters face the challenge of returning to those habitats after completing their larval development. The ability of these larvae to locate suitable habitat in which to settle is critical to their subsequent successful survival and recruitment into the adult population (Cowen et al., 2007; Pineda et al., 2007). A number of studies have demonstrated that the larvae of many marine species are not simple passive drifting particles, but rather they can actively control their dispersal and settlement, in combination with oceanographic transport (Kingsford et al., 2002; Poulin et al., 2002; Fiksen et al., 2007; Manriquez and Castilla, 2011). However, in most marine species the relative importance of larval behaviour and the physical mechanisms involved in larval transport to coastal habitats is still not clearly understood, despite being critical to the development of realistic dispersal and population models that would be useful for the management of economically important species (Cowen et al., 2006; Staaterman and Paris, 2014).

The southern rock lobster (SRL), *Jasus edwardsii*, supports valuable commercial and recreational fisheries in southern Australia and in New Zealand. The larval phase in this species

is one of the longest pelagic larval durations of any marine species, lasting 18-24 months as phyllosoma stages (Booth, 2006). These are typically most abundant in waters 100's of km offshore (Booth and Phillips, 1994; Chiswell et al., 2003). The phyllosoma larvae of *J. edwardsii* have limited or no horizontal swimming capacity with oceanic currents and eddies thought to be the most important factors involved in their transport (Bruce et al., 2000; Bruce et al., 2007). After 11 phyllosoma developmental stages, the larvae metamorphose to a puerulus stage as far as 200 km offshore and then actively swim shoreward to settle (McWilliam and Phillips, 1997; Jeffs et al., 1999; Jeffs et al., 2001a). The mechanism by which the pueruli move inshore is unclear, but it is likely that directed onshore orientation by pueruli helps to guide a combination of the use of natural onshore advection and active swimming (Booth, 2001; Chiswell et al., 2003; Jeffs et al., 2005; Linnane et al., 2010b). The research presented in this thesis examined settlement processes through a combination of analyses of existing data and structured laboratory and field experiments.

Natural onshore advection

The settlement of pueruli on artificial crevice collectors has been measured continuously at many sites throughout the geographical range of the SRL for more than 30 years in an effort to begin to understand long term recruitment patterns (Cohen and Gardner, 2007; Booth and McKenzie, 2009; Linnane et al., 2014). The magnitude of pueruli settlement is highly variable among sites and years, but there is a relatively consistent seasonal trend with lower settlement during autumn and settlement peaks in winter (the main one) and summer (Booth, 1994; Cohen and Gardner, 2007; Linnane et al., 2010b). In South Australia and in New Zealand, wind stress, Ekman transport and storm events have been linked to fluctuations in the settlement of SRL pueruli, suggesting that local process can be important (Booth et al., 2000; Linnane et al., 2010b). However, there has not been an examination at a large geographical scale of the

settlement of SRL to investigate synchronicity and the broad-scale environmental drivers. Additionally, in Tasmania the relationship between local environmental variables and pattern of settlement has not been studied.

In organisms with lengthy larval periods such as SRL, spatial patterns of larval dispersal are particularly difficult to determine, but examining the synchronicity of localised settlement over a range of spatial scales can provide insights into the factors influencing dispersal and settlement processes (Paradis et al., 2000; Liebhold et al., 2004; Broitman et al., 2008). Synchronicity in settlement over large geographic scales suggests that broad-scale environmental processes are operating to determine the magnitude of settlement in the same larval pool, while a lack of synchrony suggests that localised processes, such as larval behaviour or small scale transport mechanisms, may be more important (Keough, 1983; Pineda, 1994; Manderson, 2008). Therefore, by examining variation in settlement covering larger spatial scales it is possible to infer the nature of factors that influence settlement and the spatial scale over which they operate (Broitman et al., 2008; Mazzuco et al., 2015).

Active onshore orientation

It has been suggested that the pueruli of SRL may use a combination of orientation cues to guide their onshore migration (Jeffs et al., 2005). Underwater sound has been recognized as a candidate for onshore orientation among some pelagic organisms, because it can be detected from relatively long distances and can provide a direction cue (Au and Hastings, 2009; Radford et al., 2011b). Recent studies show strong differences in the spectral and temporal composition of ambient sound associated with different coastal habitats which has the potential to also provide a remote cue on the quality of habitat at the sound source (Radford et al., 2010; Nedelec et al., 2015). Some pelagic organisms can detect underwater sound and change their orientation to reach their preferred habitat (Montgomery et al., 2006). For instance, crab megalopae (5

species) exposed to a typical coastal reef sound showed marked changes in swimming behaviour and a significant reduction in their time taken to complete metamorphosis, suggesting that ambient underwater sound is an important settlement cue for these crab species (Stanley et al., 2010). No behavioural experiments exploring the ability of *J. edwardsii* or other spiny lobster species to detect and orientate to underwater sound have been reported. However, underwater sound was implicated as a possible cause for more than 4,000 pueruli caught in the seawater intake of a power station on the west coast of New Zealand (Booth, 1989; Jeffs et al., 2005), and recently underwater sound from reefs was found to advance the physiological development of pueruli to juveniles (Stanley et al., 2015).

While underwater sound can be detected from long distances and can be used as an important signal for orientation (Atema et al., 2012; Paris et al., 2013), chemical cues may also be an indicator for important habitat characteristics (e.g., available food or presence-absence of conspecifics and predators) (Gebauer et al., 2002; Horner et al., 2006; Goldstein and Butler, 2009; Huijbers et al., 2012; Tapia-Lewin and Pardo, 2014). Reef habitats are characterized by a unique suite of organisms (e.g., macroalgae) that may have unique chemical signatures which could be used as a settlement cue (Forward et al., 2003; Goldstein and Butler, 2009). There is limited empirical evidence showing chemotaxis for habitat selection by SRL pueruli, but an extensive number of chemosensory sensilla are found in their antennae and antennules (Jeffs et al., 1997; Cox and Bruce, 2003), suggesting that they could discriminate between different chemical cues (Butler et al., 1999; Booth, 2001). For example, pueruli of the Caribbean spiny lobster, *Panulirus argus*, are attracted to coastal chemical cues including from the red algae *Laurencia* spp. which also hasten the development of pueruli to benthic juveniles (Goldstein and Butler, 2009).

Habitat selection and post settlement survival

The first few days immediately post-settlement in SRL is a period of high mortality due to predation by fish, octopus, crabs and other lobsters (Edmunds, 1995; Mills et al., 2005; Mills et al., 2006; Mills et al., 2008). The early benthic phase in SRL has cryptic coloration and nocturnal behavior which make it difficult to investigate their ecological interactions (Butler et al., 2006). Nevertheless, laboratory experiments and some field observations suggest that early juveniles actively search for crevices and individual horizontal holes (Butler et al., 1999), and they eat small fauna (Edmunds, 1995; Frusher et al., 1999; Booth, 2001; Caputi et al., 2013). This is potentially important in the context of climate change because one of the effects in the eastern coast of Tasmania has been the depletion of kelp forests due to both a range extension of the long-spined sea urchin, *Centrostephanus rodgersii*, and also the southward penetration of the warm and nutrient poor East Australian Current (EAC) (Ling, 2008; Johnson et al., 2011). In north-eastern Tasmania there is a negative relationship between the abundance of the urchin, *C. rodgersii,* and the abundance of the sub-adult lobsters of *J. edwardsii,* which is causing concerns for the potential impact of this habitat change on lobster productivity (Johnson et al., 2011). Lower density of lobsters in this habitat could be because of either lower settlement or lower survival post-settlement. Survival may be affected by the presence of kelp due to protection from predation during periods of nocturnal activity, as well as a potential source of food because of their associated fauna.

In summary, the research summarized in this thesis investigated mechanisms involved during the settlement process and the post-settlement survival of SRL. The interaction with kelp was explored in an attempt to identify possible effects of climate change on this species. The research presented in this thesis examines three aims (Figure 1.1): to A) identify relationships among environmental variables and settlement of SRL at both local and regional

scales from long-term SRL settlement monitoring data sets taken throughout the range of this species; B) experimentally determine the behavioural response of SRL puerulus to environmental cues (i.e., chemical cues and reef sound) that may influence their spatial patterns and success at settlement; and C) experimentally determine the effect of climate-change induced habitat changes on coastal reefs to the settlement and post-settlement survival of SRL in Tasmania.

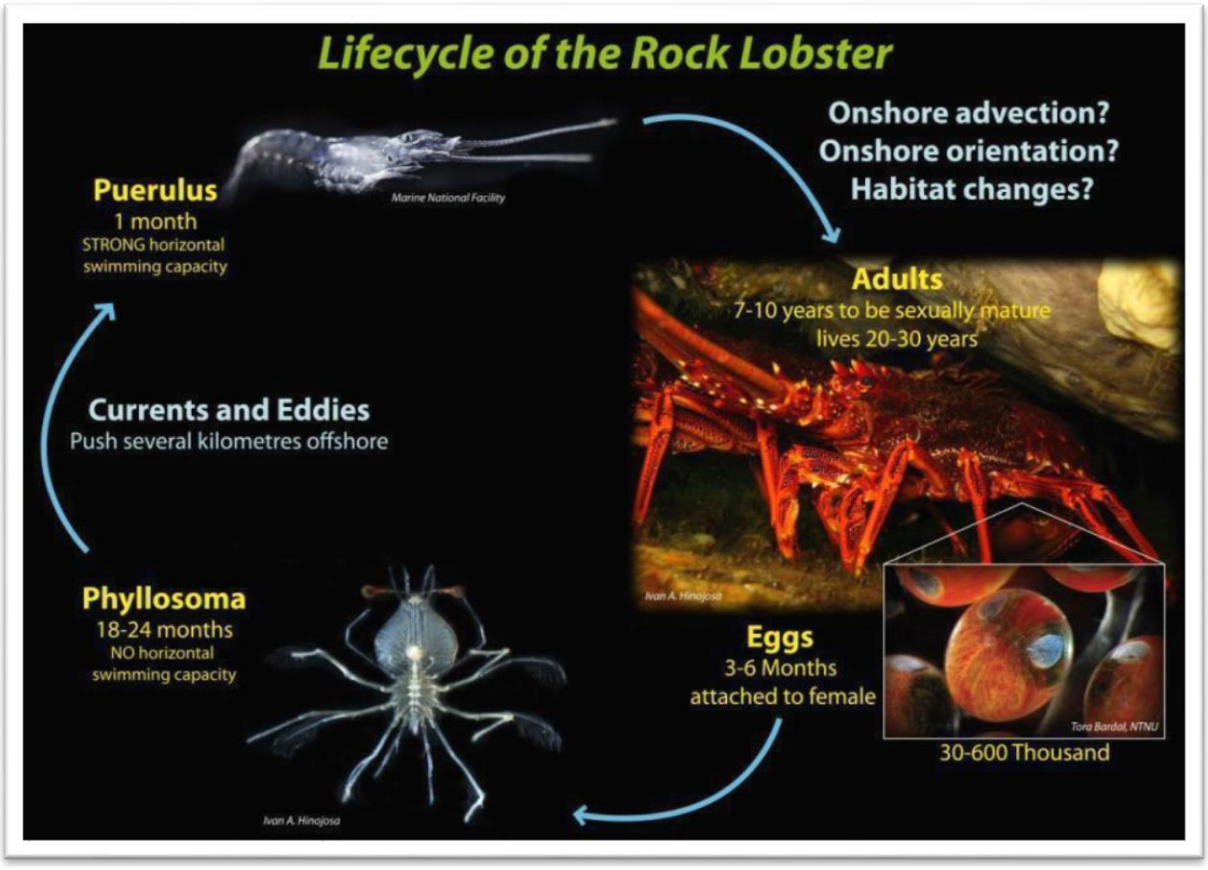


Figure 1.1. Lifecycle of the southern rock lobster, *Jasus edwardsii*, highlighting the questions addressed through the research presented in this thesis.

1.1 Thesis structure

This thesis has been prepared as a series of stand-alone manuscripts for submission to scientific journals. Consequently, there is some repetition of information among chapters that could not be avoided without losing the integrity of the research.

Chapter 1. A general introduction providing the contextual information of the research presented in the thesis and identifying the major gaps in the field and how they will be addressed.

Chapter 2. This chapter examines the environmental drivers of SRL pueruli settlement at regional and local scales for Southern Australia and New Zealand.

Chapter 3. This investigates the behaviour of SRL pueruli in response to different habitat-associated chemical cues and whether the development of pueruli to juvenile is accelerated in the presence of chemical cues associated with coastal waters in laboratory experiments.

Chapter 4. The research presented in this chapter examines whether pueruli can detect underwater sound as a directional cue for orientation to settlement sites by using an *in-situ* behavioural experiment in New Zealand.

Chapter 5. In this chapter the effect of climate-driven decline of kelp habitats on SRL settlement and post-settlement survival is examined.

Chapter 6. General discussion summarising the main findings of the research presented in the thesis and providing recommendations for future research directions.

Chapter 2:
Broad scale patterns and environmental drivers of settlement in the southern rock lobster, *Jasus edwardsii*

This work has been prepared for submission to Fisheries Oceanography as:

Hinojosa, IA, Gardner C, Green BS, Jeffs AG, Leon R & Linnane A. Broad scale patterns and environmental drivers of settlement in the southern rock lobster, Jasus edwardsii.

Crevice collector used to monitor settlement of *Jasus edwardsii*.

"In spiny lobster we might expect relative low proportional losses to predation during the long larval period, high losses during advection, and higher recruitment variability" J. Stanley Cobb (1997).

2.1 Abstract

Temporal and spatial settlement trends of the southern rock lobster, *Jasus edwardsii* were examined to identify the processes regulating the magnitude of settlement of pueruli. Settlement data were collected from 1994 to 2011 along the Southern Australian and New Zealand coasts and the influence of environmental variables on these settlement trends was examined over different spatial scales. Using Dynamic Factor Analysis, we identified common settlement trends at a regional scale (100-500 km): the magnitude of settlement at sites from South Australia and Victoria were similar, but different to sites in Tasmania. In New Zealand, three spatial regions were identified with differences in the magnitude of puerulus settlement among northern, middle and southern sites. Least squares models were used to examine whether environmental processes including climate/ocean forcing indices (Southern Oscillation, SOI; Dipole Mode, DMI; and Southern Hemisphere Annular Mode, SAM) explained trends in the magnitude of settlement for each region. Higher puerulus settlement in South Australia, Victoria and in the middle region of New Zealand appeared to occur in years with higher rainfall and storms in spring (negative DMI and SAM) and El Niño conditions (negative SOI). In Tasmania and in southern sites from New Zealand, higher settlement occurs during opposite conditions of La Niña. To examine the influence of local processes on settlement magnitude in Australian sites, we correlated local settlement magnitude with local environmental variables using dynamic regression modelling. These models were able to explain only a small proportion of the settlement variability, but higher wave period and wind relaxation were relatively more important than the sea surface temperature in South Australia and Victoria. In Tasmania, the Zeehan Current transport appears to control the settlement of the southern sites, while at the east coast the East Australian Current transport influenced puerulus settlement. Overall, the results suggest that settlement over large scales (100-500's km) is modulated by oceanic processes measured with SOI, DMI and SAM indices but

outcomes vary between regions. At a local scale, waves, wind strength and current appear to have some influence on pueruli transport. Much of the settlement variability was not explained by changes in environmental variables suggesting that settlement in *Jasus edwardsii* is a complex process where larval behaviour, biological factors such as larval production, predation and food supply, and oceanographic process might interact at different scales. The apparently complex processes affecting settlement strength showed that environmental conditions that reduce settlement strength in one region of the fishery often increase settlement strength in other regions. This could provide resilience to climate change and other environmental pertubations at the scale of the entire fishery.

2.2 Introduction

Settlement is the end point of the integration of many pelagic larval processes, including planktonic productivity, predation, and transport by ocean currents. These factors and others produce variability in the population dynamics of many benthic marine species (Keough and Swearer, 2007). Examining the processes which influence the spatial and temporal variability in larval settlement advances the understanding of population dynamics and can lead to the development of new predictive tools (Cowen et al., 2006). However, the processes determining the variability in larval settlement are complex and include biotic processes, such as ecological interactions that determine the size of the larval pool and larval behaviour, as well as abiotic factors, such as physical transport mechanisms (Cowen et al., 2007; Pineda et al., 2010).

In organisms with extensive larval periods, spatial patterns of dispersal are particularly difficult to determine, but examining the synchrony of settlement over a range of spatial scales can provide insights into the factors influencing dispersal and settlement processes (Paradis et al., 2000; Liebhold et al., 2004; Broitman et al., 2008). For example, synchrony in settlement

over large geographic scales suggests that broad-scale environmental processes are operating to determine the settlement magnitudes in the same larval pool, while a lack of synchrony suggests that localised processes, such as larval behaviour or small scale transport mechanisms may be more important (Keough, 1983; Pineda, 1994; Manderson, 2008). Therefore, by examining variation in settlement covering a range of spatial scales from tens of kilometres (local) to 1000's of kilometres (large) it is possible to infer the nature of factors that influence settlement and the spatial scale they operate over (e.g., Broitman et al., 2008; Colton et al., 2014; Mazzuco et al., 2015).

Jasus edwardsii, known as southern rock lobster in Australia, is broadly distributed across the southern mainland of Australia, around Tasmania and New Zealand, including the Chatham Islands in the far east of New Zealand (Booth, 2006). This species supports valuable commercial and recreational fisheries across its distribution with around 6,500 t harvested per year (Jeffs et al., 2013). An individual female can annually produce between 44,000 to 660,000 eggs during the austral winter (May to August; Green et al., 2009). In spring (September to October) the eggs hatch into the brief naupliosoma stage before an extended planktonic phyllosoma phase lasting 18-24 months, which is one of the longest pelagic larval durations of any marine species (Lesser, 1978; Bradford et al., 2015). The phyllosoma larvae are mainly influenced by large scale transport processes, such as currents and eddies, where diurnal vertical migration is believed to assist in their retention often hundreds of kilometres from benthic populations (Booth and Phillips, 1994; Chiswell and Booth, 1999; Booth and Ovenden, 2000; Bradford et al., 2005). After 11 phyllosoma developmental stages, the larvae metamorphose to a puerulus stage as far as 200 km offshore before actively swimming shoreward in search of small holes and crevices in coastal rocky reef habitats in which to settle (Jeffs et al., 2001a; Jeffs et al., 2005; Bradford et al., 2015). Settlement mainly occurs at night,

is highly seasonal, and can vary by location and magnitude from year to year (Booth et al., 2000; Cohen and Gardner, 2007; Linnane et al., 2014).

Monitoring of settlement in *J. edwardsii* on artificial collectors has been undertaken throughout their distribution range for 30–40 years and has been used as a predictor of future recruitment to fishable biomass in some regions (Gardner et al., 2001; Booth and McKenzie, 2009; Linnane et al., 2010b; Linnane et al., 2014). Monitoring of settlement in other spiny lobster fisheries has enabled the identification of environmental signals affecting settlement (Caputi, 2008; but see de Lestang et al., 2015) and the impact of changes in the size of the adult breeding population (e.g., Ehrhardt and Fitchett, 2010). Therefore, identifying any environmental and population variables that are driving settlement variability of *Jasus edwardsii* is of interest for the management system of this valuable fishery resource.

Data from regional monitoring of settlement in *J. edwardsii* has been used in previous research on environmental processes in driving settlement variability. For example, discrete projects at spatial scale or time series in both South Australia and New Zealand found that wind stress, Ekman transport and storm events associated with El Niño events can be related to seasonality and pulses of settlement (Booth et al., 2000; Linnane et al., 2010b). At other locations, environmental variables influencing fluctuations in settlement have proven to be more difficult to isolate (e.g., Hayakawa et al., 1990; Bruce et al., 2007). This may be partly due to the large geographical distribution of this species which includes complex current systems which involve the convergence of different water masses, especially in Tasmanian waters (Tilburg et al., 2001; Ridgway and Condie, 2004; Oliver and Holbrook, 2014).

In the present study settlement data covering 17 years from 13 sites throughout the range of *J. edwardsii* across the coast of Australia and New Zealand were analysed for the first time in an effort to: 1) test for the presence of any broad scale settlement trends across this large geographical scale (>1,000s km); 2) test for regional scale settlement trends (~500's km) and

correlation with climate/ocean forcing indexes, and; 3) test for potential environmental variables that influence variability at the local scale of settlement (<10's km) for Australian sites only.

2.3 Methods

Settlement data

Settlement magnitude of *Jasus edwardsii* has been monitored monthly by fisheries management agencies in Australia and in New Zealand from the early 1990's by counting pueruli and early juveniles in sets of crevice collectors (Booth and Tarring, 1986) usually deployed on sand adjacent to shallow coastal reefs (Cohen and Gardner, 2007; Booth and McKenzie, 2009; Linnane et al., 2014). Crevice collectors consist of angled plywood sheets that mimic natural crevice habitat, and the monthly survey procedures involve a diver who first placed a mesh bag around the collector and then hauled it to the surface for counting the catch (Booth and Tarring, 1986). This study used settlement data consisting of monthly counts of pueruli and early juveniles in collectors from seven monitoring sites in Australia and six sites in New Zealand (Figure 2.1) for the period 1994 to 2012. In Australia, the data were collected from three sites in South Australia (Beachport (A); Livingston Bay (B); and Blackfellows Caves (C)); one site in Victoria (Port Campbell (D)) and three sites in Tasmania (Recherche Bay (E); South Arm (F) and Bicheno (G). Data from New Zealand was from Stewart Island (Halfmoon Bay (H)), two sites on the east coast of the South Island (Moeraki (I); and Kaikoura (J)), and three sites from the east coast of the North Island (Castle Point (K); Napier (L) and Gisborne (M)) (Figure 2.1). An index of settlement from each site was determined as the mean number of pueruli and early juveniles per collector per month. To compare trends among sites, each data time series was scaled (i.e., standardized).

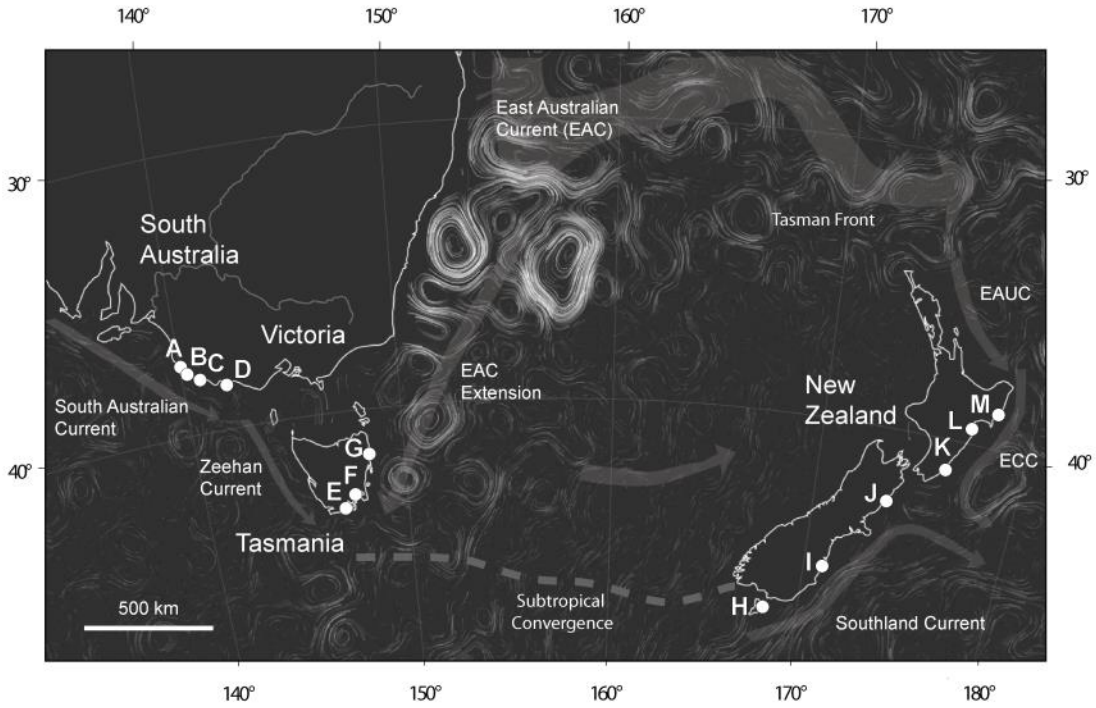


Figure 2.1. Settlement monitoring sites in South Australia (A-C), Victoria (D), Tasmania (E-F) and New Zealand (H-M). Arrows represent the main sea surface transport. EAUC is East Auckland Current and ECC East Cape Current (from Cresswell, 2000; Oliver and Holbrook, 2014). Background image represented in white lines modelled sea surface currents from http://earth.nullschool.net/ (May 2015).

Broad scale settlement trends (>1,000's km).

To evaluate common trends in settlement at the scale of thousands of kilometres across the geographic range of *J. edwardsii*, a settlement index was calculated as the mean number of pueruli and juveniles per collector per three months (December to February, March to May, June to August, and September to November per year) for each sampling site and was scaled to unit of standard deviation to compare trends among sites (i.e., standardized, for each settlement value the total mean was subtracted and divided by the total standard deviation) (Figure 2.2). No missing values were allowed in the analyses explained below, so missing values on each time series (settlement index per three months) were completed using predictive mean matching procedures described in Little (1988) and using the "BaBooN" package for "R" (Meinfelder, 2011). This is an imputation method that combines parametric and non parametric

techniques to generate reliable and weighted predicted values based on the inverse of the covariance matrix of the residuals from the regression of these variables (i.e., time versus settlement index) on the completed data (Meinfelder, 2011). Common trends in the settlement index among sites were identified using dynamic factor analysis (DFA), which is a multivariate time-series analysis technique used to estimate underlying common patterns in a set of time series, whilst also considering autocorrelation effects which are not incorporated into other common analytical approaches that are widely used, such as principal component analysis or correspondence analysis (Zuur et al., 2003). DFA is an effective approach for reliably identifying common trends within biological time series data (Zuur and Pierce, 2004; Erzini, 2005; Katara et al., 2011; Colton et al., 2014; Castillo-Jordan et al., 2015). DFA was conducted utilizing the "MARSS" package for "R" software (Holmes et al., 2012). The level parameters (loadings) indicated the relationships within the time series, with positive and negative loadings representing positive and negative correlations with DFA trends respectively. The magnitude of the level parameters reflects the amount of variance explained by the model trend. Three forms of the observation error variance and covariance were tested: (1) the same variance and no covariance (diagonal and equal), (2) different variances and no covariance (diagonal and unequal), and (3) the same variances and covariance (equalvarcov). Akaike's information criterion (AIC_c) was used to determine which models were best for describing the numbers of common settlement trends, and the two best models are presented herein.

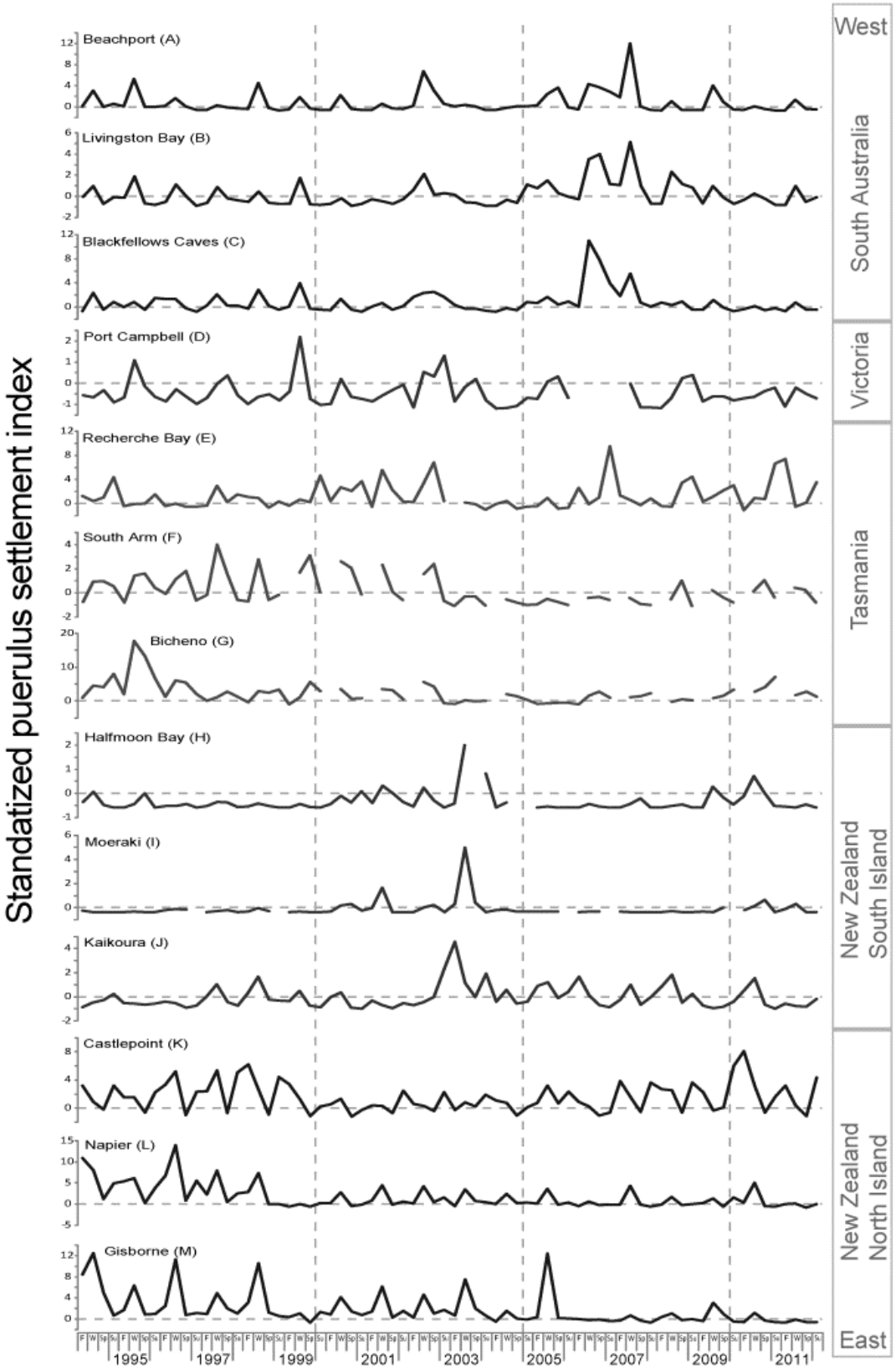


Figure 2.2. Time series of the standardised settlement of *J. edwardsii* per three months at thirteen sites along South Australia, Victoria, Tasmania and New Zealand. Sites are arranged west to east from top to bottom

Regional scale settlement trends (500's km) and climate-ocean indexes

To explore the regional scale of common trends in settlement among Australian and New Zealand sites separately, two sets of DFA were conducted independently for each country using the same settlement index per site as in the previous analyses for broad scale patterns. The common trends in settlement identified for the analyses for both countries were correlated with climate/ocean forcing indices utilizing generalised least squares models (GLS) to identify if these processes influenced the magnitude of settlement at this scale. The GLS technique estimates the unknown parameters in a linear regression model when the variances of the observations are unequal (heteroscedasticity), or when there is a certain degree of correlation between the observations (autocorrelation) (Pinheiro et al., 2015). These analyses were conducted with "nlme" package for "R". The climate/ocean forcing indexes used were the Southern Oscillation Index (SOI), the Dipole Mode Index (DMI or Indian Ocean Dipole), and the Southern Hemisphere Annular Mode Index (SAM). All of these indices have a significant regional influence on the ocean and coastal climate conditions in the southern part of Australia and around New Zealand.

The SOI gives an indication of the development and intensity of El Niño or La Niña events in the Pacific Ocean. The SOI is calculated using the pressure differences between Tahiti and Darwin which impacts the strength of the Pacific trade winds and the sea surface temperatures along the equator. Negative values of the SOI indicate El Niño episodes, whereas positive values are typical of La Niña. The two extremes of this oscillation affect the winter/spring rainfall over much of south-eastern Australia through storm activity and fronts with higher rainfall expected during La Niña events (Cai et al., 2011) (www.bom.gov). In New Zealand, El Niño conditions result in intensification of southerly winds in winter/spring, while north-easterly winds are more characteristic during La Niña (Gordon, 1985; Jiang et al., 2013)

(www.niwa.co.nz). SOI data was acquired from ftp.bom.gov.au/anon/home/ncc/www/sco/soi/soiplaintext.html.

DMI (or IOD) is a coupled ocean and atmosphere phenomenon in the equatorial Indian Ocean that affects the climate of the Southern Hemisphere, including that of Australia and New Zealand in winter/spring (Saji et al., 1999; Ashok and Saji, 2007). It is measured by the difference between sea surface temperature anomalies in the western and eastern equatorial Indian Ocean. A positive period is characterised by cooler than normal water in the tropical eastern Indian Ocean and warmer than normal water in the tropical western Indian Ocean. A positive pattern is associated with a decrease in rainfall (weaker westerlies and storms) over southern Australia and part of New Zealand, and some, but not all, occur during the same years as El Niño (Ashok et al., 2007). Negative values of DMI often result in an increase of rainfall and storm activities over parts of southern Australia and the northern part of New Zealand, which can also be associated with La Niña, but the relationship between SOI and the DMI is not clear (Saji et al., 1999; Meyers et al., 2007; Schott et al., 2009). DMI data was extracted from http://www.jamstec.go.jp/frcgc/research/d1/iod/HTML/Dipole%20Mode%20Index.html

The SAM explains the relative position of the westerly wind belt (northern or southern) that circles Antarctica (Marshall, 2003). The changing position of the westerly wind belt influences the strength and position of cold fronts and mid-latitude storm systems. A positive phase of SAM occurs when the position of the westerly wind belt is contracted towards Antarctica generating weaker than normal westerly winds and higher pressures over southern Australia that restricts the penetration of cold fronts, and hence producing more easterly winds from the Tasman Sea, while in New Zealand it is associated with relatively light winds and settled weather. A negative SAM occurs when the position of the westerly wind belt moves toward the equator which results in more and stronger storms, and low pressure systems over

southern Australia and New Zealand (Marshall, 2003; Renwick and Thompson, 2006) (see also http://www.bom.gov.au/). SAM data was obtained from http://www.nerc-bas.ac.uk/icd/gjma/sam.html

Local scale settlement trends (10's km) and environmental variables in Australia

We examined settlement trends for each site within Australia in relation to local environmental variables. A monthly settlement index was used and missing months were in-filled using a predictive mean matching procedure as previously outlined (Little, 1988). To identify local environmental factors that correlate with the monthly settlement index, dynamic regression modelling (DRM) was used. DRM takes into account information from past observations (autocorrelation) of the time series and also incorporates external variables (environmental factors) that may explain trends in the time series (Hyndman and Athanasopoulos, 2014). These analyses were conducted using "lmtest" and "leaps" packages for "R", as the "leaps" package "*performs an exhaustive search for the best subsets of the variables in "x" for predicting "y" in linear regression, using an efficient branch-and-bound algorithm*" (Miller, 2002; Hothorn et al., 2013; Lumley, 2013). The environmental variables used in the DRM analyses were the monthly average of local wind speed (strength), the westerly and southerly components of the wind (u and v components respectively), monthly average of waves (height and period), and the monthly average of the sea surface temperature (SST).

Local winds (u and v components and strength) and waves (height and period) were extracted from the National Oceanic and Atmospheric Administration (NOAA) WAVEWATCH III (NWW3) regional model (http://polar.ncep.noaa.gov/waves/product_table.shtml?-multi_1-) and adjusted to ½ degree fishing blocks. The SST data were derived from the Pathfinder sensors on the NOAA satellites, where combined nighttime and daytime

passes were quality controlled and composited to obtain a monthly average. Data were obtained at a spatial resolution of 0.036° Latitude by 0.042° Longitude and then adjusted to ½ degree fishing blocks. The geographical position of the fishing blocks used to extract these data is presented in the supplementary material.

The three settlement sites from Tasmania were also correlated with the monthly average of the net current transport around the island in another set of DRM analyses. Along the west coast of Tasmania the Zeehan Current (ZC) flows southward, which has a very similar water composition to the South Australian Current (Ridgway and Condie, 2004). The ZC spreads beyond the southern tip of Tasmania reaching the southern portion of the east coast of the island during the winter in some years (South Cape flow, SC) (Cresswell, 2000) (Figure 2.1). The east coast of Tasmania is mainly influenced by an extension of the East Australian Current (EAC), which is a complex and highly energetic system with large mesoscale eddies flowing southward mainly during summer (Ridgway and Dunn, 2003). The EAC separates from the Australian coast forming an eastward outflow along the Tasman Front (Boland and Church, 1981; Oliver and Holbrook, 2014) (Figure 2.1)

Current transport around Tasmania was obtained from the Bluelink ReANalysis model (BRAN 3p5 in http://wp.csiro.au/bluelink/global/bran/) described by Oke et al. (2013). Three sections perpendicular to coast were selected; one in the west, other in the south and the other east coast (supplementary material). Monthly minimum, maximum and mean current speeds across each section were extracted from 1993 to 2011. Negative values in EAC and ZC represented southward flow and positive values in SC values represented eastward flow.

2.4 Results

Broad scale settlement trends (>1,000's km)

Patterns in *J. edwardsii* settlement among all sites and overall years showed a clear aggregation at a regional scale (100-500's km). Two DFA models were identified as highly parsimonious based on the AIC_c criteria (both models with same variance and no covariance); one model presented three settlement trends (Model A), and the other model showed four settlement trends (Model B) (Figure 2.3). Both models identified similar trends and grouped the sites correspondingly. Trend 1 in both models showed relatively steady increase in settlement throughout years until 2006-07 and grouped adjacent sites located in South Australia and Victoria (Sites A – D, factor loading > 0.4) (Figure 2.3A&B). Trend 2 in Model A and Trend 3 in Model B presented highest settlement around 2004 grouping sites located in New Zealand, mainly in the South Island (site H- I, factor loading > 0.4) and, also the northern site of the North Island (M, factor loading > 0.4) (Figure 2.3A). Trend 3 in Model A, where the highest settlement occurred around 1995-96, can be interpreted as a broad pattern among the sites, but with exceptions at some sites (E, H-K). Trend 2 in Model B suggested that when higher settlement occurred in Tasmanian sites (E-G) there was lower settlement in middle sites of New Zealand (J-L) or *vice versa* (Figure 2.3B). This regional aggregation was consistent and also can be visualised plotting the loading of Trend 1 and 2 in both models (Figure 2.3A & B).

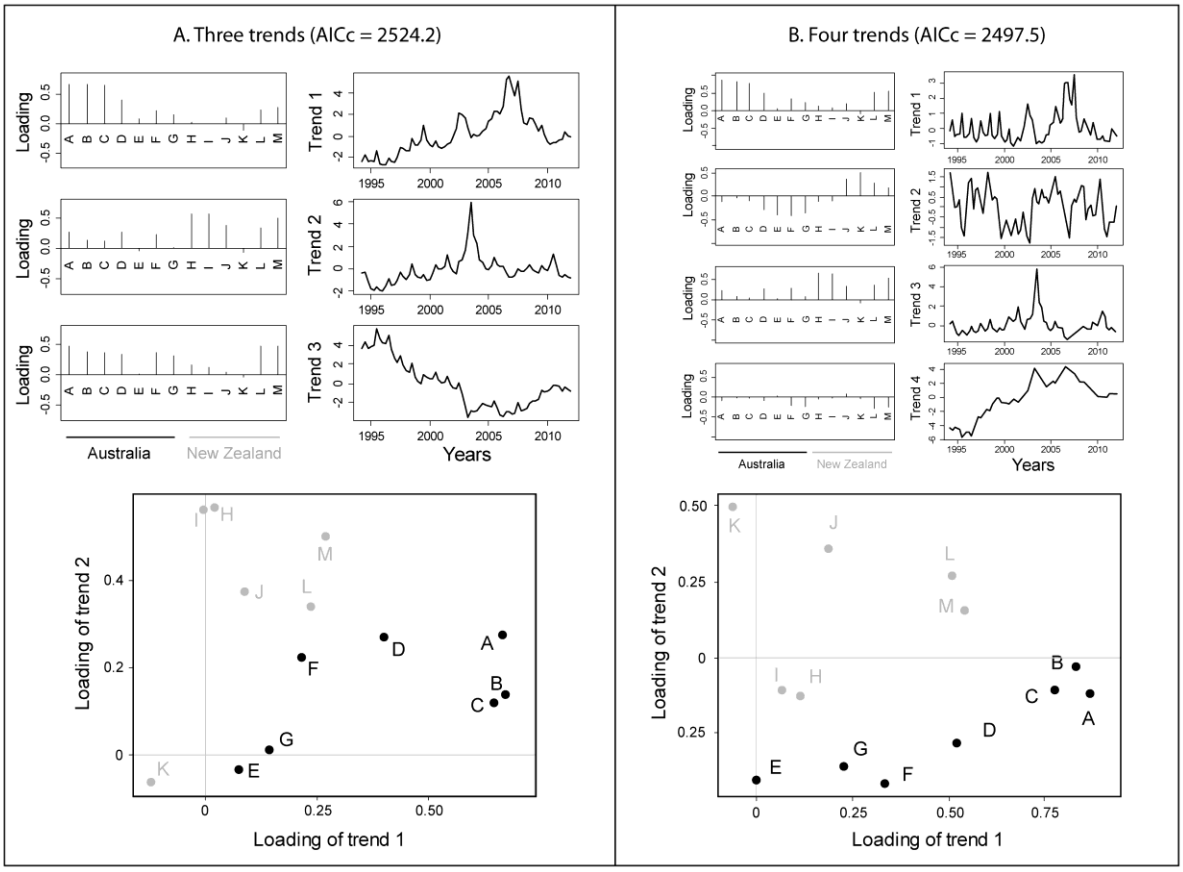


Figure 2.3. Dynamic Factor Analysis (DFA) of the time series of *J. edwardsii* settlement among sites from Australia and New Zealand. The best two models based on AICc values are shown. A. Model with three trends in settlement, and B. model with four trends. The equivalent loading for each site (A-M from the left site) on the common trend are shown. Biplots between loadings from the first two trends in both models are also shown to highlight segregation by country on the settlement trends.

Regional scale settlement trends (500's km) and climate-ocean indexes

Australian sites: Trends in *J. edwardsii* settlement showed a similar regional aggregation to previous analysis in Australian sites. The most parsimonious model identified was with three settlement trends with same variance and no covariance (Figure 2.4A): settlement in South Australia and Victoria (A-D) was reflected on Trend 1; also, settlement from Victoria (D) and in one site from Tasmania (F) was described by Trend 2, but with negative loadings; Trend 3 showed the settlement in one sites from Tasmania (G) (Figure 2.4A). One site from Tasmania (E) had an independent settlement trend that was not apparent in this model.

The GLS models including the climate ocean forcing indexes explained 38 to 79% of the settlement trends variability (Table 2.1). Overall, the results suggested that higher settlement in Australian sites was influenced by higher rainfall (storm activity) during winter/spring (negative DMI index), but was also influenced by SOI and SAM indexes in different combinations (Table 2.1). Trend 1 was negatively correlated with SOI which means that higher settlement is influenced during El Niño event (Table 2.1). Trend 2 was also negatively correlated with SOI and positively correlated with SAM, but interpreting the negative value in loadings (Figure 2.4A), higher settlement was influenced by La Niña conditions with a greater number of stronger westerly storms (Table 2.1). Finally, Trend 3 was positively correlated with SOI, where higher settlement was also expected during La Niña conditions (Table 2.1).

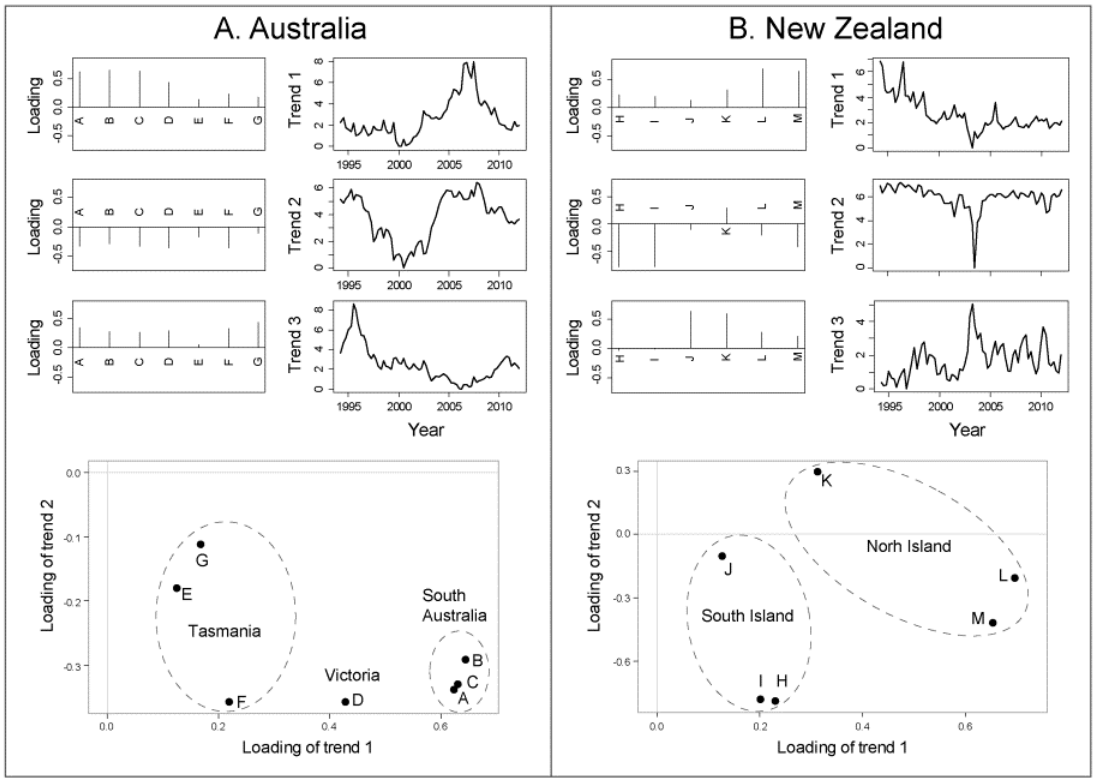


Figure 2.4. Dynamic Factor Analyses (DFA) conducted on the time series of *J. edwardsii* settlement among sites from: A. Australia; and B. New Zealand separately. The model with three trends in settlement had the best AIC in both analyses. The equivalent loading for each site (A-G and H to M respectively) of the common trend are shown. Biplots between the site loadings from the first two trends respectively also are shown to highlight segregation of the settlement trends.

New Zealand sites: A model with three settlement trends was identified with the lowest AIC_c values with the same variance and no covariance (Figure 2.4B). This suggested a clear and feasible regional aggregation of settlement trends. Trend 1 represented the settlement in two northern sites of the North Island (L and M); Trend 2 represented the settlement in the two southern sites of the South Island (H and I), but with negative values in loading (i.e. higher settlement in those sites around 2004). Trend 3 represented the middle region of the New Zealand fishery and aggregated the northern site of the South Island (J) and the southern site from the North Island (K) (Figure 2.4B).

The GLS models including the climate ocean forcing indexes explained only 11 to 41% of the variability in settlement (Table 2.1). Overall, the SOI index influenced the settlement in the southern and middle part of New Zealand. The settlement shown by Trend 1 was not influenced by any of the climate ocean forcing indices tested (Table 2.1). The settlement represented in Trend 2 was negatively correlated with SOI index, suggesting higher settlement during La Niña conditions (notice the negative loading in Figure 2.4B). Trend 3 was negatively correlated with SOI and positively correlated with DMI with higher settlement influenced by El Niño conditions and weaker westerly winds and storms.

Table 2.1. Least squares model (GLS) testing of the effect of the Southern Oscillation Index (SOI), the Dipole Mode Index (DMI), and the Southern Hemisphere Annular Mode Index (SAM) on common trends in pueruli settlement in Australia and New Zealand (see Figure 2.4).

complete model= Model:TRENDS~SOI*DMI*SAM

	Trends	Oceanic index							
		SOI	DMI	SAM	SOI:DMI	SOI:SAM	DMI:SAM	SOI:DMI:SAM	
					P	P	P	P	r^2
Australia	1 (sites A-D)	-	-		**0.01**	0.85	0.08	0.62	-0.42
	2 (sites D&F)	-	+	+	**0.03**	0.70	**<0.001**	0.06	-0.79
	3 (sites F&G)	+	-		**<0.001**	**<0.001**	**0.04**	0.76	-0.38
New Zealand	1 (Northern L&M)				0.50	0.07	0.56	0.67	-0.18
	2 (Southern H&I)	-			**0.05**	0.15	0.29	0.99	-0.11
	3 (Middle J&K)	-	+		**<0.001**	**<0.001**	0.36	0.91	-0.41

Local scale settlement (10's km) and environmental variables in Australia

Overall, calm winds and higher wave periods appeared relatively more important that local sea surface temperature (SST) in terms of influence on local *J. edwardsii* settlement. However, some of the Dynamic Regression Models (DRM) explained only a low proportion of the settlement variability (Table 2.2). In southern Australia, higher wave periods and wind strength explained more of the monthly settlement variability than other variables included in the models (Table 2.2 and Supplementary material). At Beachport (A) 53% of the settlement variability was explained by the model, but only 8% of the variance was explained by higher wave period one month lagged (Table 2.2). With sites from South Australia and Victoria (B-D), the wind strength was inversely correlated with settlement strength and explained only 8 to 15 % of the model variability with some months lagged (Table 2.2). At Livingston Bay (B) the sea surface temperature (SST) appeared to have some effect on settlement, but only explained around 8% of the variance (Table 2.2). Models for two sites from Tasmania (E & F) explained less than 36% of the variability with higher wave period and wind strength (v component) more important than other environmental variables (16 and 17% of the model). At Bicheno (G), the model explained around 50% of the variability with higher wave period lagged 5 and 3 months explaining 14% of the model variability in combination (Table 2.2).

In Tasmanian sites the models conducted with current transport only explained less than 40% of the monthly settlement variability (Table 2.3). Patterns in the effect of current strength were logical suggesting that these were not spurious patterns - the Zeehan Current (ZC) appeared to have some influence in the settlement in the southern sites (E and F) while the East Australian Current (EAC) appeared to influenced settlement on the east coast (site G, Table 2.3 and Supplementary material). At the most southern site (Recheche Bay, E), higher southward transport of the ZC lagged by 4 months explained 12% of the model. At South Arm (F), the ZC appeared to have some influence in combination with a westward flow of the SC

(29% in combination). A lower variability of the EAC explained 10% of the settlement variability at Bicheno (Table 2.3). Overall, the current transport models explained only a small proportion of the variability in pueruli settlement which suggests that other environmental or biological factors may be important determinants of the strength of the monthly settlement variability.

Table 2.2. Dynamic Regression Models (DRM) testing wind (u and v components and strength), waves (height and period) and sea surface temperature (SST) on the monthly puerulus settlement in Australian sites. Only the three most significant factors are shown. (L) represents number of months lagged; (+) or (-) the positive or negative correlation effect; and (%) the percentage of the variance explained. Full results and model validation are provided in supplementary material.

Sites	Adj. R^2	F	P	FACTORS		
Beachport (A)	0.534	18.1	<0.001	Wave period (L1)(+)(8%)	Wind u (L0)(+)(6%)	Wind strength (L4)(-)(5%)
Livingston Bay (B)	0.439	11.6	<0.001	Wind strength (L9)(-)(14%)	SST (L7)(+)(8%)	SST (L2)(-)(6%)
Blackfellows Caves (C)	0.396	14.9	<0.001	Wind strength (L3)(-)(15%)	Wind u (L0)(+)(7%)	
Port Campbell (D)	0.606	21.8	<0.001	Wind strength (L9)(-)(8%)	Wind strength (L7)(+)(7%)	Wind v (L8)(+)(6%)
Recherche Bay (E)	0.261	6.3	<0.001	Wave period (L2)(+)(16%)	Wind v (L1)(+)(10%)	Wave height (L4)(+)(10%)
South Arm (F)	0.365	8.1	<0.001	Wind v (L8)(-)(17%)	Wave period (L0)(+)(12%)	Wind u (L5)(-)(10%)
Bicheno (G)	0.516	27.4	<0.001	Wave period (L5)(+)(8%)	Wave period (L3)(-)(6%)	

Table 2.3. Dynamic Regression Models (DRM) testing transport by the Zeehan Current (ZC), flow off the southern tip of Tasmania (SC), and the East Australian Current extension (EAC) on monthly puerulus settlement at Tasmanian sites. Only the three most significant factors are shown. (L) represents number of months lagged and (%) the percentage of the variance explained. Full results and model validation are provided in supplementary material.

Sites	Adj. R^2	F	P	FACTORS		
Recherche Bay (E)	0.358	15.2	<0.001	ZC southward (L4)(12%)	ZC low var. (L3)(8%)	SC high var. (L2)(5%)
South Arm (F)	0.224	7.63	<0.001	ZC low var. (L3)(17%)	SC westward (L4)(12%)	ZC mean (L1)(10%)
Bicheno (G)	0.384	16.9	<0.001	EAC low var. (L1)(10%)	ZC low var. (L4)(6%)	SC high var. (L0)(5%)

2.5 Discussion

The settlement of *J. edwardsii* showed regional synchrony across scales of around 100-500's km, with wherein processes related to El Niño/La Niña events (SOI) and westerly storms and rainfall (DMI and SAM) having a common influence. For Australian sites, settlement appeared to be influenced by some local environmental factors to various extents including wave period, wind strength, and current transport direction, while sea surface temperatures tended to be less important. Environmental factors examined in this study explained only a low proportion of the settlement variability indicating that settlement is driven by complex processes and other environmental factors or biological features not examined here are also relevant.

Synchronism on settlement at spatial scales

Coherence or synchrony in settlement patterns across locations (>100 km's) have been identified in spiny lobster species suggesting that large-scale oceanographic processes often drive changes in levels of puerulus settlement (Booth, 1994; Caputi, 2008; Linnane et al., 2014). For example, spatio-temporal settlement patterns in western rock lobster, *Panulirus cygnus*, have been shown to be influenced by the strength of the Leeuwin Current, where strong current transport influenced by La Niña conditions have been associated with above-average settlement simultaneously in several sites (Caputi, 2008). However, during recent years lower settlement of *P. cygnus*, has been recorded despite La Niña conditions, suggesting that other factors may be involved, such as changes in the timing of egg hatching relative to storm events, and shifts in offshore sea surface temperature that could influence the larval development (de Lestang et al., 2015). Here, we found that common trends in settlement had a regional component (100-500 km) where settlement was also influenced by the El Niño/La Niña events (SOI) in combination with westerly storms in most sites (DMI and SAM indices).

Factors affecting settlement trends were not consistent across all regions with trends in the northern two sites from New Zealand (Napier and Gisborne, L and M respectively) apparently unrelated to indices of oceanic processes. Booth et al., (2000) suggested that the favourable conditions for settlement along the east coast of the North Island are southerly winds and storms which enhance the westward Ekman drift in the upper layer of the ocean. Southerly wind intensification in New Zealand is expected during El Niño conditions (Gordon, 1985). Our models suggested higher puerulus settlement during the El Niño conditions in the north-east of the South Island and in the south-east of the North Island (Kaikoura and Castle Point, J and K respectively); the model explained 41% of the settlement variability at those sites. In contrast, the settlement in the southern sites of the South Island (Halfmoon Bay and Moeraki, H and I respectively) appeared to be higher during La Niña conditions where north-easterly wind anomalies are typical, probably transporting the pueruli to the southern sites. Although an apparent effect of La Niña was detected, most of the settlement variability could not be explained by the model for the southern sites of New Zealand.

Across South Australia (sites A-C) and Victoria (site D), similar trends of puerulus settlement were revealed by this study as per analyses conducted by Linnane et al (2014). In another study Linnane et al. (2010b) reported that westerly winds and Ekman transport, which are dominant during winter, appear to influence the seasonal settlement patterns across this area. Here we also found that higher rainfall during winter/spring and higher storm activity (negative DMI) and El Niño events (negative SOI) contributed to higher settlement in South Australia and Victoria. Settlement of pueruli at the Tasmanian southern site (Recherche Bay, E) did not have any common trends with the other two Tasmanian sites. However, settlement at South Arm (F) and Bicheno (G) were relatively similar and had higher settlement during La Niña conditions.

Overall, our analyses suggest that large-scale oceanographic processes appear to affect settlement strength over scales of 100-500 km for both countries. These analyses suggested that during El Niño events the south-westerly wind anomalies transport the pueruli to the north; in contrast during La Niña events the north-easterly wind anomalies transport the pueruli further south in the whole study area. Strong anomalies on the wind-driven surface currents not only have some influence on *J. edwardsii* but also in other spiny lobsters. For example, in the Caribbean spiny lobster, *P. argus,* fluctuations in puerulus settlement are correlated with hurricanes and associated sea level changes (Briones-Fourzan et al., 2008).

Local environmental factors controlling the settlement

Evidence for onshore transport of pueruli of spiny lobsters by localised physical processes has typically involved weak correlations between the magnitude of pueruli arrivals and onshore physical processes (Phillips et al., 2006) and our study is not an exception. Surveys of the distribution of pueruli suggests their abundance offshore plus active onshore movement can be important (Chiswell and Booth, 1999; Jeffs et al., 2001a). Consequently, settlement strength appears to be the result of a combination of active onshore swimming and passive transport processes (Briones-Fourzan et al., 2008; Goldstein and Butler, 2009; Linnane et al., 2010b). Transport by wind-driven surface currents has been proposed as an influence of settlement magnitude of *J. edwardsii* in South Australia and New Zealand (Booth et al., 2000; Linnane et al., 2010b). However, examination of daily pueruli settlement data from Castle Point, New Zealand, did not reveal a relationship between puerulus settlement and local environmental variables, including wind direction (Hayakawa et al., 1990). Our models including local environmental variables at a monthly scale was intended to provide information on the processes of transport from oceanic areas to coastal reef but we were able to explain only a low proportion of the settlement variation. At Beachport (site A, South Australia) higher

wave period (wave direction was not included in the analysis) showed a positive influence on settlement when lagged by one month, which could be explained by the benefit that Stoke's drift may deliver for onshore movement of pueruli. However, a negative influence of the wind strength, nine and three months lagged, in the other two sites from South Australia and in Port Campbell (Victoria) suggests that calm conditions in previous months may also have some influence during the phyllosoma transport and the relative position of the larval pool. For Tasmanian sites, environmental variables explained an even lower proportion of the settlement variability, but again wave period and wind across the main shore direction may benefit pueruli transport and result in a small increase in settlement. In Tasmania, environmental variables related to local current transport explained around a third of the variability in local settlement (<38%) but processes were mixed between sites. At Recherche Bay (E) settlement was influenced by the southern transport of the ZC from the west coast, whereas at Bicheno (G) the strength of the southward flowing EAC led to increase in pueruli settlement. The small proportion of the settlement explained by models using local environmental variables indicates that other environmental factors not examined here are likely to be relevant to the puerulus onshore transport, including more chaotic environmental processes, such as fronts or eddy positions.

Processes affecting active onshore swimming by puerulus could also play a role independently of physical processes. The pueruli of *J. edwardsii* can swim at velocities of 10-40 cm s^{-1} for sustained periods providing the capacity to move considerable distances shoreward (Jeffs et al., 1999; Jeffs et al., 2001b; Wilkin and Jeffs, 2011). A number of potential orientation cues have been suggested to guide this active orientation shoreward (Jeffs et al., 2005). Recently, underwater sound from reefs was found to advance the physiological development of pueruli to juveniles, implying pueruli have the capacity for sound detection (Stanley et al., 2015). While some research has been conducted on orientation cues of pueruli,

there is still much uncertainty and scope for more research. Chemical cues derived from suitable settlement habitats were found to elicit a chemotactic response in the pueruli of *P. argus* (Goldstein and Butler, 2009). Higher concentrations of pueruli of *P. cygnus* have been found at the surface of the sea in rough sea conditions, leading to speculation that they could be using wave directional cues, such as Stoke's drift (Phillips et al., 1978). Similarly, *in situ* experiments on tethered pueruli of *P. argus* found they were orientating in response to wind direction as well as tidal flow (Kough et al., 2014). Consequently, it is possible that pueruli of *J. edwardsii* may use some of these directional cues, or others, in combination with physical transport as waves, currents and winds.

Fishery implications

This study suggests that large scale oceanographic processes, modulated by SOI, DMI and SAM, lead to common patterns in settlement at a regional scale (100-500 km). The regional settlement trends identified here show that pueruli monitoring programs across multiple sites at a regional scale are an effective tool for evaluating settlement trends rather than using the comparatively noisy data from a single site, although the southern site from Tasmania (Recherche Bay, E) had a distinct settlement pattern.

The mechanism by which these large scale processes affect settlement strength is not clear, but could be through both changes in abundance and/or phyllosoma transport and position. Large scale processes may also be affecting settlement strength through influences on egg production and timing of the larval release, food for larvae availability and larval mortality, as was recently suggested for *P. cygnus* (de Lestang et al., 2015). Settlement patterns are also likely to be influenced by physiological and behavioural processes, including triggers for phyllosoma metamorphosing to pueruli, and influences on their active onshore swimming which can be assisted or impeded by waves, winds and currents. Settlement in *J. edwardsii* is

clearly a complex process and it was apparent that oceanographic processes interact at different scales and the effect varies between regions. Large scale oceanographic processes or environmental factors that were positive for settlement in one region often had the opposite effect in other areas. This suggests resilience of the fishery to climate change across the scale of the broader Australian and New Zealand Fishery.

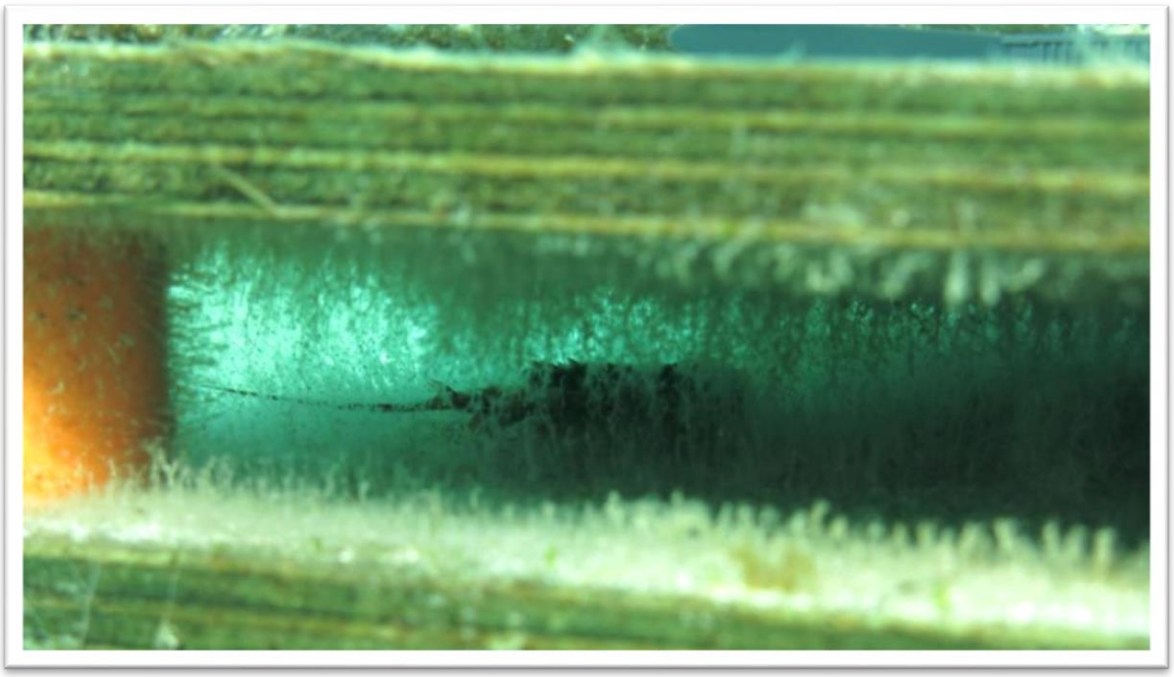
2.6 Acknowledgements

We are grateful to Klass Hartmann and Craig Mundy who provided the wave and SST satellite data. We also thank Eric Oliver who extracted the current transport data from around Tasmania. Funding for this research has been provided by the PhD scholarship BECAS-Chile programme to I.A.H., the Australian Research Council Linkage project (Project No. LP120200164) from B.S.G. and C.G., the ANZ Trustees programme "Holsworth Wildlife Research Endowment".

Chapter 3:
Coastal chemical cues for settlement in the southern rock lobster, *Jasus edwardsii*

This work has been prepared for submission to Marine Biology as:

Hinojosa IA, Gardner C, Green BS & Jeffs AG. Coastal chemical cues for settlement in the southern rock lobster, Jasus edwardsii



Puerulus stage III of *Jasus edwardsii* in a crevice collector.

"A benthic animal with a planktonic larval stage is a strange beast. Not only must it survive and prosper in two different realms but it must also successfully make the transitions to the plankton and back to the benthos"

G.A. Jackson (1986).

3.1 Abstract

Larval behaviour plays an important role in dispersal and settlement, with cues from the environment providing crucial guidance to these processes. The post-larval, or puerulus stage, of the southern rock lobster, *Jasus edwardsii*, are known to migrate from oceanic water and settle on coastal reefs using a combination of onshore transport and active swimming. In laboratory experiments, we examined environmental cues used for this migration, specifically whether chemical cues in coastal waters versus oceanic water influenced their swimming orientation and their rate of development to juveniles. Sixty six percent of pueruli actively swam toward coastal water rather than oceanic water (n = 41), indicating that they may use some chemical cues to orientate their swimming from offshore waters. Holding pueruli in coastal water versus artificial seawater did not expedite the development of pueruli to benthic juvenile stage, indicating that other cues could be important to the final settlement process. This study suggests that chemical cues are used for orientation during the onshore migration to settlement sites in this valuable species.

3.2 Introduction

Many marine invertebrates and fish species have a pelagic larval phase that lasts from several days to several months and is the primary dispersal phase among localised benthic populations (Shanks, 2009). The dispersal ability of marine species is essential for persistence of local populations and therefore understanding the processes involved during dispersal is often useful for management and conservation (Cowen et al., 2007; Pineda et al., 2010). Larval behaviour and response to environmental cues have an important role during dispersal especially in relation to successfully finding a suitable habitat to settle (Kingsford et al., 2002; Cowen and Sponaugle, 2009). Consequently, understanding larval sensory capabilities, the identity of behavioural cues and the corresponding larval behavioural response are valuable for developing realistic dispersal and recruitment models (Levin, 2006; Staaterman and Paris, 2014).

Spiny lobsters (Decapoda; Palinuridae) have some of the most long-lived larvae among the marine invertebrates (4 to 24 months, Phillips et al., 2006; Bradford et al., 2015). The pelagic larval phase ends with metamorphosis to a non-feeding post-larva, known as a puerulus (Jeffs and Holland, 2000; Phillips et al., 2006). The southern rock lobster, *Jasus edwardsii*, is broadly distributed from the southern mainland of Australia, around Tasmania, to New Zealand, supporting valuable fisheries with around 6,500 t harvested per year (Booth, 2006; Jeffs et al., 2013). The larval biology of the species is poorly understood because of the logistic difficulties of sampling these animals due their low density and distribution beyond the continental shelf, although there have been some empirical observations of their distribution and behaviour (Bruce et al., 2000; Bradford et al., 2005; Wilkin and Jeffs, 2011). The pueruli of *J. edwardsii*, as in other spiny lobster species, appear to be only active at night and have been observed swimming in straight lines at the sea surface (Jeffs and Holland, 2000). Horizontal swimming speeds of pueruli of 10 to 40 cm s^{-1} have been estimated from laboratory

studies (Jeffs and Holland, 2000; Wilkin and Jeffs, 2011). There is some evidence that movement of pueruli of *J. edwardsii* across the continental shelf can be influenced by large scale transport processes such as Ekman Current transport associated with along shore winds (Linnane et al., 2010b). However, it has been difficult to find significant correlations between numbers of settling pueruli and environmental variables over shorter periods (e.g., daily settlement) and smaller spatial scales (Hayakawa et al., 1990). This lack of correlation and the shoreward directed distribution of pueruli has been used to suggest that active swimming dominates the onshore migration, with effective orientation guided by environmental cues, such as underwater sound, magnetic fields, physical cues, celestial cues and water chemistry (Jeffs et al., 2005; Phillips et al., 2006). However, there is little hard evidence to support this proposition (Jeffs et al., 2005; Stanley et al., 2015).

Chemical signals, or cues, play diverse and complex ecological roles in aquatic systems (Atema et al., 2012), particularly in crustacean species (reviewed in Breithaupt and Thiel, 2012). This includes the use of chemical signals from nursery habitats in navigation and settlement of larvae (Gebauer et al., 2002; Forward et al., 2003; Paul et al., 2011; Tapia-Lewin and Pardo, 2014). For example, premolt megalopae of the blue crab *Callinectes sapidus* orient toward nursery areas by swimming upstream in response to cues from aquatic vegetation (Forward et al., 2003). Estuarine decapod species may accelerate metamorphosis from megalopae to juvenile in the presence of humic acids (Gebauer et al., 2003). Chemical cues for settlement have also been reported from lobsters, with pueruli of the Caribbean spiny lobster, *Panulirus argus*, found to be attracted to chemical cues from coastal waters containing chemicals from the red algae *Laurencia* spp. and this also hastens their development to benthic juveniles (Goldstein and Butler, 2009). Results from a field study off eastern Tasmania, Australia, appeared to be consistent with the use of chemical cues from the giant kelp, *Macrocytis pyrifera*, by pueruli of *J. edwardsii* (Hinojosa et al., 2015). However, a laboratory

experiment did not find differences in the timing of the development of pueruli to juvenile in the presence of the brown algae *Carpophyllum maschalocarpum* versus bare rock, although development for both treatments was faster than for a sand treatment (Stanley et al., 2015). This result suggests that chemical cues do not accelerate development of the pueruli of *J. edwardsii* to juvenile, although whether or not pueruli adjusted their swimming behaviour based on chemical cues was not examined. Therefore, the aim of this study was to use laboratory experiments to determine whether *J. edwardsii* pueruli have an orientation response to chemical cues in seawater that would have the potential to be used by pueruli to guide their orientation to coastal habitats and expedite their development to juveniles.

3.3 Materials and Methods

The ability of pueruli of *Jasus edwardsii* to identify chemicals cues for settlement was evaluated in two sets of laboratory experiments. One experiment examined whether the timetable of pueruli development to juvenile is fixed or is a plastic response to chemical cues in seawater. The second set of experiments tested whether the directional swimming behaviour of the pueruli was influenced by different water sources. The two sets of experiments were conducted between July 2012 and February 2014 at the Institute for Marine and Antarctic Studies Laboratory (IMAS) at Taroona, Tasmania (Figure 3.1).

Source of pueruli

Pueruli of *J. edwardsii* were collected monthly (July to February) using 18 crevice collectors deployed at Bicheno on the east coast of Tasmania (41.8713° S, 148.3024° E; Figure 3.1). Additionally, during the settlement season of 2014, pueruli catches from 24 extra collectors at Bicheno, 12 collectors at Recherche Bay (43.5938° S, 146.9187° E); and 16

collectors at South Arm (43.0530°S, 147.4169°E) were incorporated (Figure 3.1). The crevice collectors were similar in design to that described and illustrated by Booth and Tarring (1986) and are used in Australia for pueruli settlement monitoring programs for fisheries management (Cohen and Gardner, 2007; Booth and McKenzie, 2009; Linnane et al., 2014). The collectors consisted of angled plywood sheets that mimicked natural crevice habitat, and the monthly survey involved a diver placing a mesh bag around the collector before it was hauled to the surface for cleaning and counting the pueruli enclosed. The live pueruli were immediately stored in seawater in an 80 l plastic drum and transported to Taroona the same day or the following morning. At the laboratory, pueruli were sorted into different stages following the schema of Booth (2001) (Table 3.1). Only "stage I" pueruli were retained and used in experiments.

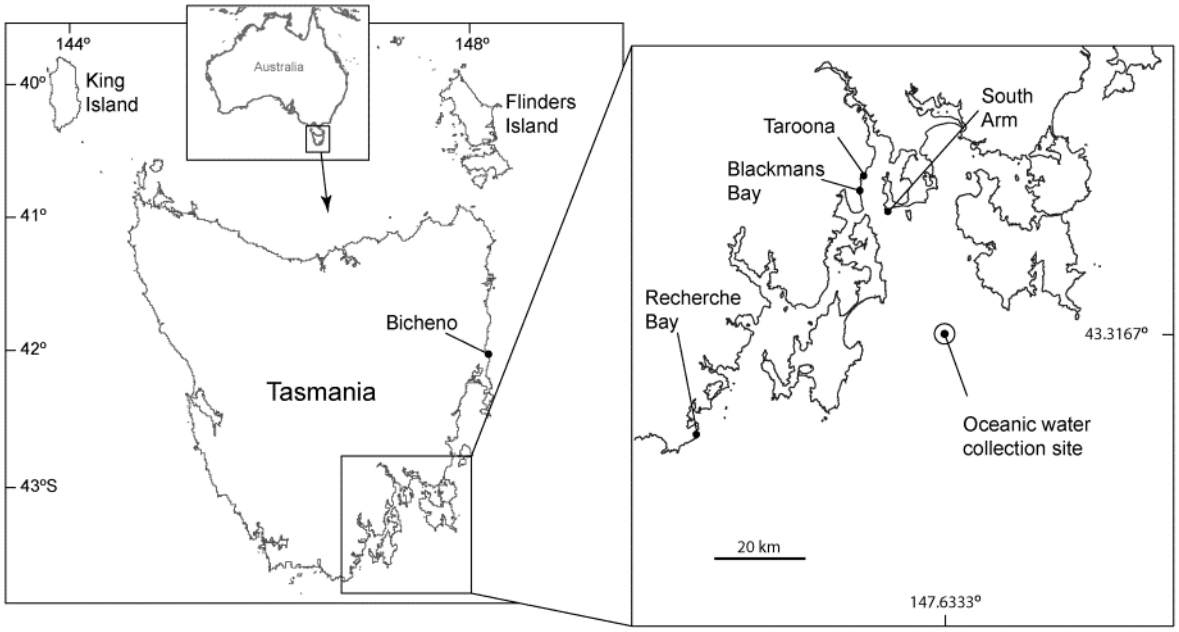


Figure 3.1. Map of Tasmania, Australia, indicating the locations used for the collection of pueruli (Bicheno, Recherche Bay and South Arm), the location of the laboratory (Taroona), the collection site for *Macrocystis pyrifera* (Blackmans Bay), and the collection site for oceanic water 20 km offshore. The oceanic water was collected at 15 m depth to avoid any potential surface water containing outflow with a freshwater influence.

Time to development and moulting

In July 2013 twenty "stage I" pueruli were sorted and retained individually in numbered plastic containers of 500 ml with a piece of plastic mesh (1 mm) in the bottom as substrate. Ten containers were filled with unfiltered seawater pumped from ~15 m depth at Taroona Bay (coastal water, SW) and the other ten containers were filled with artificial seawater (Instant Ocean®, ASW). The containers were all held in a running bath of seawater (70 l) to maintain the water temperature in the plastic containers at ambient seawater temperature (11.8 ± 0.4 °C, mean ± SD) and were maintained under natural winter light period (11 h light:13 h dark). The seawater in each numbered container was changed every 24 h and the salinity of the ASW was adjusted accordingly to the natural salinity variation of SW (34.4 ± 0.8 ppt; pH = 7.8 ± 0.2). Five to six hours before seawater changes, the ASW was prepared by using ultrafiltered tap water (0.05 µm) and actively mixing Instant Ocean® until no salt remained, followed by high aeration. Every 24 h the pueruli were staged until all pueruli had moulted to first instar juveniles (Table 3.1).

Table 3.1. Pueruli development and stages used sensu Booth (2001).

Puerulus stages	Description
I	Completely transparent
I-II	Hepatopancreas faintly visible
II	Hepatopancreas clearly visible
II-III	Pigmentation in the antennae and cephalothorax
III(-)	Pigmentation starting in the abdomen
III	Full pigmentation in cephalothorax and abdomen
III(+)	Dark coloration and orange colours in pereiopods
Juvenile instar 1	Moulting process, loss of large pleopods

Two events were measured and compared between treatments: 1) time of the pigmentation starting in the abdomen (change from "stage II-III" to "stage III(-)"), and 2) timing of the moulting process (III(+) to Juvenile instar 1)(Table 3.1). To compare the probability of pueruli remaining as stage "II-III" and "III(+)" between SW and ASW

treatments, the Kaplan-Meier survival curves were estimated using "R" software (R Development Core Team, 2008) and the "survival" package (Therneau, 2015). The Kaplan-Meier survival test examines the probability in time of an event occurring and the differences between treatments was estimated using the G-rho family test (Harrington and Fleming, 1982; Crawley, 2013).

Directional swimming behaviour

Chemotactic responses of pueruli for four different water masses were tested at night using four replicate binary choice chambers similar in design to that described in Goldstein and Butler (2009) and consisted of a white PVC tube (15 cm internal diameter, 100 cm long) with a lid in each end (Figure 3.2). The tube was cut from above forming a "U" shape where a gap of 13 cm in width along the tube was generated. At 20 cm from both ends of the tube a plastic funnel was inserted to produce a central arena of 60 cm in length with two chambers behind the funnels at each end (Figure 3.2). The seawater tested was supplied from two header tanks (80 l) that flowed into each chamber at opposite ends of the tube via a 0.4 cm internal diameter pipe at a flow rate of 0.3 l min^{-1} (0.2 to 0.5 l min^{-1}). Dye solutions were initially used to confirm even flow of the two water sources and mixing in the choice arena.

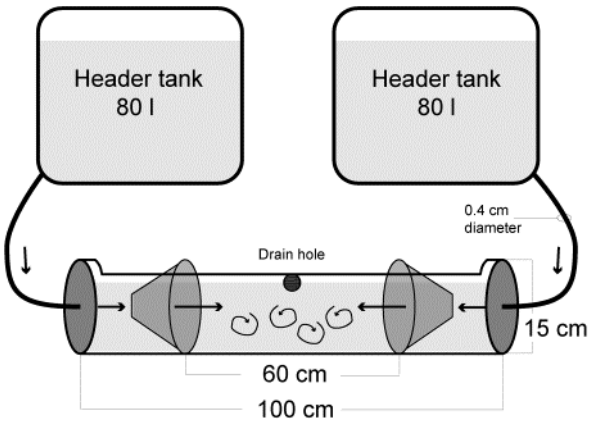


Figure 3.2. Behavioural binary choice chamber for pueruli given a choice between water sources. Arrows indicate the flow of water.

Four water sources were used in the experiments: 1) coastal seawater (SW), which consisted of seawater pumped from 15 m depth at Taroona (salinity = 33.0 ± 0.4 ppt; mean ± SD); 2) coastal seawater, which had been passed through a 30-50 μm sand filter to exclude any potential food particles; 3) coastal seawater plus giant kelp, *Macrocystis pyrifera*; and 4) oceanic seawater collected from 20 km offshore and pumped from 15 m depth (salinity = 34.7 ± 0.5 ppt) (43.3367º S; 147.6333º E, Figure 3.1). To prepare the *M. pyrifera* seawater solution, fresh kelp were collected 24 to 48 h prior to the experiment from Blackmans and Recherche Bays (Figure 3.1). Around one kilogram (1,180 ± 428 g, mean ± SD) of the kelp was placed in a monofilament mesh bag and was added to the header tank filled with 80 l of coastal water for 10-12 hours before experiments to enable leaching of any exudates from the kelp. Only kelp blades were used in this experiment that were previously washed and cleaned of epiphytes and debris in running coastal water. To control for any possible chemical effect due to the plastic mesh bag, a clean mesh bag was added to the header tank of the opposing treatment. Experiments were run for three combinations of seawater sources: 1) coastal seawater (SW) vs. sand filtered costal seawater; 2) coastal seawater (SW) vs. coastal seawater with *M. pyrifera* exudates; and 3) coastal seawater (SW) vs. oceanic seawater. The seawater in the header tanks were filled 10 to 12 hours before experimentation to allow the water temperature to stabilise to ambient (12 to 15 °C).

Upon arrival at the laboratory, stage I pueruli were immediately transferred to individual 40 ml jars with perforated lids within a 400 l tank supplied by flow through ambient seawater before being used in experiments the same night (4-6 h after arrival). Experiments were conducted at night and involved allowing water from the header tanks to flow into the chamber. Individual pueruli were introduced to the central arena in an individual jar, which was opened and positioned facing down in the centre of the choice chamber. After 10 min the jar was removed permitting the puerulus to make a directional choice by swimming through

one of the funnels at either side of the chamber. Every 10-20 min the position of the puerulus in the chamber was examined and the experiment was finished when the puerulus became trapped in one of the two sides of the chamber, or after two hours if the puerulus had not moved into either of the chambers. The preparation of the materials and observations were conducted with red light illumination (Kodak Wratten Gelatin Filter #29; >600 nm). The allocation of seawater treatment to header tanks was randomised for each replicate run of the choice chamber. The chambers, mesh bags and header tanks were washed thoroughly between each run with fresh water to remove any residual chemicals from the previous replicate run. To test whether the choice of seawater source by pueruli was non-random, a simple goodness-of-fit test was used, with the null hypothesis being the expected frequency of an equal preference for both sides of the choice chamber (Quinn and Keough, 2002). The data from all trials were considered as observed frequency in the test (Quinn and Keough, 2002).

3.4 Results

Time to development and moulting

There was no significant difference in the time taken by pueruli of *J. edwardsii* to pass through their development for the two water treatments ($p > 0.05$; Figure 3.3). On average, pueruli stayed at "stage II-III" for 12 ± 4 days (mean ± SD, n = 10) before developing pigmentation in the abdomen in ASW and 9 ± 3 days (n = 10) in SW ($\chi^2 = 3.3$; $P = 0.07$). Pueruli in SW took 20 ± 3 days (n = 10) to moult to juvenile and 21±3 days (n = 10) in ASW ($\chi^2 = 0.2$; $P = 0.63$). There were no significant differences in water temperature (11.7 ± 0.4 °C), salinity (34.4 ± 0.7 ppt), or pH (7.9 ± 0.2) between the two water treatments ($P > 0.1$). However, all the pueruli in ASW died during the moulting process indicating that it was unsuitable for

use in the following behavioural experiments. All the pueruli in SW successfully moulted to juvenile.

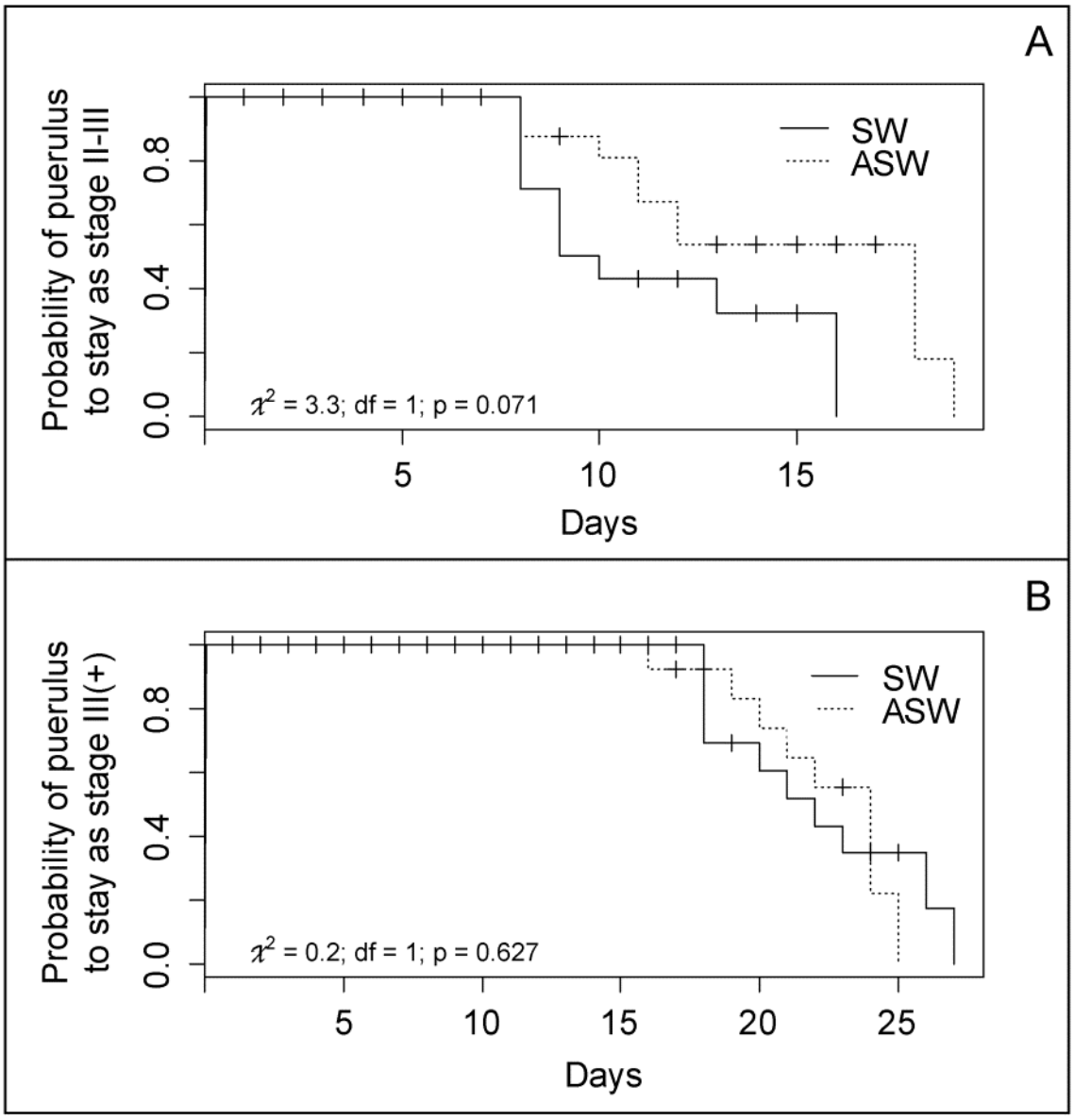


Figure 3.3. (A) Daily probabilities of pueruli staying as "stage II-III", and (B) probability of pueruli staying as "stage III (+)" in coastal seawater (SW) from Taroona Bay versus in artificial seawater (ASW). Probabilities were estimated and tested with Kaplan-Meier survival test. Pueruli in the treatment with ASW died during the moulting process.

Directional swimming behaviour of the pueruli

Relatively more pueruli (66%) of *J. edwardsii* moved toward coastal water compared with oceanic water (34%) (χ^2 = 4.1; P = 0.04). Similarly, more of the pueruli (64%) moved toward coastal water than towards coastal water with enhanced exudates from *M. pyrifera* (36%) (χ^2 = 4.4; P = 0.04). Pueruli did not show a significant preference to move toward either filtered or unfiltered coastal water (χ^2 = 0.2; P = 0.68) which excludes the possibility that pueruli were attracted by potential food particles in the water solution (Figure 3.4). Overall, pueruli of *J. edwardsii* exhibited a preference for coastal waters but the presence of additional kelp exudates reduced this attraction.

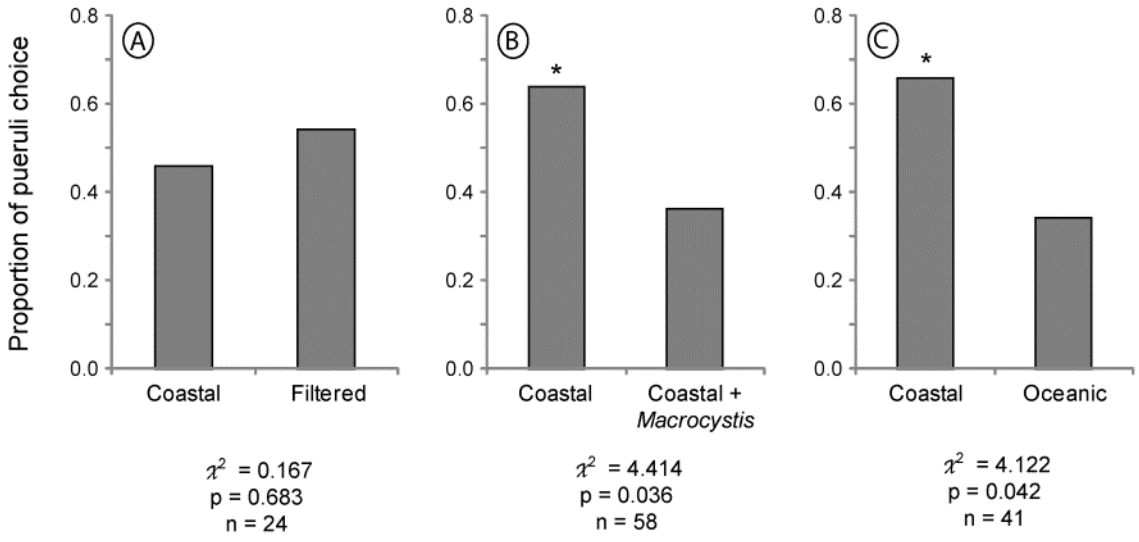


Figure 3.4. Proportion of pueruli of *J. edwardsii* choosing to swim toward different seawater sources in the binary choice chamber experiments: A) coastal seawater versus filtered seawater; B) coastal seawater versus coastal seawater containing exudates from *M. pyriferas*; and C) coastal seawater versus oceanic seawater. Degrees of freedom was equal to 1 for each simple goodness-of-fit test.

3.5 Discussion

Results of this study show that pueruli of *J. edwardsii* actively moved towards coastal water when offered a choice of coastal or oceanic water, suggesting that they may use chemical cues to orientate their onshore swimming. However, coastal waters did not hasten the development of pueruli to benthic juvenile stage, indicating that other cues could be important to the final settlement process, or that chemical cues are not involved in this process. Previous experiments on *J. edwardsii* pueruli found that the development of pueruli to juvenile was accelerated when exposed to either a brown algae, *Carpophyllum maschalocarpum*, or bare rocks when compared to sandy substrate, suggesting that their development may be substrate dependent (Stanley et al., 2015). Development may be triggered by a complex interaction between a range of factors as underwater sound from settlement habitats has also been shown to advance the development of pueruli to first instar juvenile in this species (Stanley et al., 2015).

Evidence of pueruli using chemical cues from coastal waters have also been found for the Caribbean spiny lobster, *P. argus*, where pueruli were attracted to and developed faster in coastal seawater and seawater containing red macroalgae, which is characteristic of their preferred settlement habitat (Goldstein and Butler, 2009). Pueruli of *J. edwardsii* settle into a range of habitats where holes and crevices are available (Edmunds, 1995; Butler et al., 2006). Therefore, it is possible that pueruli of this species respond to less specific chemical cues to development than the pueruli of *P. argus*. However, changes in the water chemistry composition from oceanic to coastal water may stimulate a behavioural response of pueruli to direct their swimming onshore rather than expediting their physiological development toward moulting to become a benthic juvenile.

The phyllosoma of *J. edwardsii* metamorphose to pueruli as far as 200 km offshore (Jeffs et al., 2001a) and have been observed swimming in straight lines at the sea surface at

night (Jeffs and Holland, 2000). Pueruli are a non-feeding (lecithotrophic) stage that depend only on the energy reserves stored during the preceding phyllosoma phase, so the duration is constrained by these limited energy reserves (Jeffs et al., 1999; Fitzgibbon et al., 2014). Therefore, any cue that assists puerulus to travel more rapidly or directly to reef habitats would be expected to increase survival and have selective advantage (e.g. Gebauer et al., 2003). Our results contribute to the growing body of evidence that movement of pueruli from offshore to settlement habitat is influenced by coastal chemical cues in combination with other cues (Jeffs et al., 2005). For example, in situ observations of pueruli of the Caribbean spiny lobster demonstrated that swimming towards the coast varies with tidal phase, possibly in response to multimodal cues such as celestial, wind, acoustic and magnetic cues (Kough et al., 2014). Chemical cues emanating from coastal habitats are typically transported several kilometres offshore before dissipating, and are known to have a concentration gradient although how this would be detected and utilised for directional information is somewhat unclear (Atema et al., 2012). Alternatively, the chemical cues in coastal water may be used as a signal to pueruli to switch to other directional cues, as has been observed for some fish species (Huijbers et al., 2012; Paris et al., 2013).

Although several fish larvae and decapod crustaceans are known to respond to chemical cues from settlement habitats, very little is known about the chemical compounds involved in this recognition. For larvae attracted to reef settlement habitat, the reef's assemblage of fauna, algae and bacteria could contribute to a complex cocktail of chemical cues that are continually released and utilised by approaching larvae as a directional cue (Gebauer et al., 2003; Gerlach and Artema, 2012). Previous field experiments examining the settlement magnitude of *J. edwardsii* in collectors with either natural or artificial kelp *M. pyrifera* attached found that settlement was higher with natural kelp, which suggested that chemical cues from the kelp attracted pueruli (Hinojosa et al., 2015). In the present study *M. pyrifera* exudates appeared to

repel pueruli. Therefore, it is possible that other cues associated with natural kelp explained the differences in pueruli abundance associated with the macroalgae in the previous study. For example, in the current study we did not use the kelp holdfast to generate the chemical cues in the laboratory which is known to provide a habitat for several species (e.g. Anderson et al., 2005). Also, the concentration of exudates from the kelp used could be different to that in the natural environment. The research method used here could be applied to test the effect of different concentrations of chemical cues, or other chemical compounds from the settlement habitats. Additional research is also required to determine the range offshore over which chemicals may provide an effective orientation cue for *J. edwardsii* pueruli, which is also of interest in a range of other marine species (Lecchini et al., 2014).

This is the first attempt to identify chemical cues used by pueruli of *J. edwardsii* to orient, and we demonstrate that they can distinguish between coastal and oceanic waters. There is substantial scope for future experiments building on this research on chemical detection. For example, in a number of fish and crustacean species that use chemical cues, the sensory pathways used to find suitable settlement habitat is altered by elevated acidification levels (e.g., Briffa et al., 2012; Nilsson et al., 2012). Ocean acidification and the impact on the pueruli chemical detection have not been tested, but could affect productivity from the fishery over the next century.

The temporal and spatial pattern of settlement of *J. edwardsii* pueruli is difficult to predict, but is monitored across the range of the fishery because it is useful as a predictor of future levels of recruitment to the fishable biomass (Gardner et al., 2001; Booth and McKenzie, 2009; Linnane et al., 2014). Understanding dispersal patterns is of interest to fisheries management so understanding the type and effectiveness of orientation cues used by pueruli, and the migration pathway of the pueruli from metamorphosis to eventual settlement location has the potential to improve the predictive power of biophysical models (Kough et al., 2013;

Staaterman and Paris, 2014). This study shows the use of chemical cues during the orientation process and suggests that this orientation could affect successful settlement of this valuable species.

3.7 Acknowledgments

We thank Ruari Colquhoun, David Fallon, Kylie Cahill, Graeme Ewing, Sarah Pyke, Hugh Jones & John Keane for assistance in the field collecting pueruli. We thank also Andrew Pender & Jason Beard for providing the field trips to collect oceanic water. Funding for this research has been provided by the PhD scholarship BECAS-Chile program to I.A.H., the Australian Research Council Linkage project (Project No. LP120200164) from B.S.G, the ANZ Trustees program "Holsworth Wildlife Research Endowment."

Chapter 4: Reef sound as an orientation cue for shoreward migration by pueruli of the rock lobster, *Jasus edwardsii*.

This work is under review in PloS ONE:

Hinojosa IA, Green BS, Gardner C, Hesse J, Stanley JA & Jeffs AG. Reef sound as an orientation cue for shoreward migration by pueruli of the rock lobster, Jasus edwardsii.

Forward swimming puerulus stage I of *Jasus edwardsii*.
Modified from Marine National Facilities.

"At the present time new organisms are continually being brought to light which make noises of one sort or another, so that the old axiom "silent as the sea" must now be considered a thing of the past"

Winthrop Niles Kellogg (1953).

4.1 Abstract

The post-larval or puerulus stage of Palinuridae lobsters (spiny or rock lobsters) swim many kilometres from open oceans into coastal waters where they subsequently settle. The orientation cues used by the puerulus for this migration are unclear, but are presumed to be critical to finding a place to settle. Understanding this process may help explain the biological processes of dispersal and settlement, and be useful for developing realistic dispersal models. In this study, we examined the use of reef sound as an orientation cue by the puerulus stage of the southern rock lobster, *Jasus edwardsii*. Experiments were conducted using *in situ* binary choice chambers together with replayed recording of underwater reef sound. The experiment was conducted in a sandy lagoon under varying wind conditions. A significant proportion of puerulus (69%) swam towards the reef sound in calm wind conditions. However, in windy conditions (>25 m s^{-1}) the orientation behaviour appeared to be less consistent with the inclusion of these results reducing the overall proportion of pueruli that swam towards the reef sound (59.3%). These results resolve previous speculation that underwater reef sound is used as an orientation cue in the shoreward migration of the puerulus of spiny lobsters, and suggest that sea surface winds may moderate the ability of migrating pueruli to use this cue to locate coastal reef habitat to settle. Underwater sound may increase the chance of successful settlement and survival of this valuable species.

4.2 Introduction

The ability of post-larvae to locate suitable habitat in which to settle is critical to the successful recruitment of many marine species that have a planktonic larval dispersal stage (Cowen et al., 2006). Settlement and recruitment of larvae play a major role in structuring marine populations and are vital to population persistence (Pineda et al., 2007; Cowen et al., 2007). Recent studies have demonstrated that the larvae of many marine species do not disperse by passive drifting as was previously thought, but rather they can actively control their dispersal (Kingsford et al., 2002; Fiksen et al., 2007). Consequently, understanding the sensory abilities and cues used by larvae for actively altering their distribution are critical to the development of realistic dispersal models that have useful applications for the management of economically important species (Cowen et al., 2006; Cowen et al., 2007; Staaterman and Paris, 2014).

The southern rock lobster, *Jasus edwardsii*, is distributed across southern Australia and around the coast of New Zealand, and supports a valuable fishery with approximately 6,500 tonnes harvested per year (Jeffs et al., 2013). An individual female can produce between 44,000 and 660,000 eggs each year (Green et al., 2009) that hatch into larvae known as phyllosoma. These larval stages are influenced by ocean currents and eddies where diurnal vertical migration frequently results in their retention 100's kilometres offshore from benthic populations (Booth and Phillips, 1994; Chiswell and Booth, 1999; Booth and Ovenden, 2000). After 15-24 months and passing through 11 phyllosoma stages, the larvae metamorphose to post-larvae or pueruli up to 220 km offshore and actively swim shoreward during nights in search of coastal rocky reef habitats in which to settle (Booth and Phillips, 1994; Phillips and McWilliam, 2009; Bradford et al., 2015). The mechanisms and orientation cues that the pueruli use to direct their migration towards the coast are uncertain, but onshore advection in combination with active swimming and guidance by a variety of potential environmental cues have been suggested (Jeffs et al., 2005; Goldstein and Butler, 2009; Kough et al., 2014).

However, in situ experiments examining active orientation responses of *J. edwardsii* pueruli to particular cues have not been reported. The pelagic pueruli (stage 1; sensu schema of Booth, 2001) upon reaching the coast progresses its development through a two subsequent developmental stages over the following 1-3 weeks until moulting to become a reptant juvenile (Booth and Phillips, 1994; Fitzgibbon et al., 2014). During the puerulus phase of development individuals remain nocturnally active, swimming among localised coastal habitats at night but remaining hidden in crevices during daylight hours (Booth, 2001; Hayakawa and Nishida, 2002).

Recently the sensory abilities and the behaviour of settlement stages of a variety of marine organisms have received considerable attention, with growing evidence that underwater sound plays an important role in the onshore orientation in coral reef fishes and in the post-larvae of some crab species (Kingsford et al., 2002; Simpson et al., 2005; Radford et al., 2007). Underwater sounds emanating from inshore reefs may be detectable tens of kilometres offshore (Radford et al., 2011b) and could carry biologically significant information about the qualities of the habitat at source for those organisms possessing sufficient sensory capabilities (Kingsford et al., 2002; Mann et al., 2007; Radford et al., 2010; Nedelec et al., 2015). The ambient underwater sound emanating from coastal reefs in New Zealand and Australia which is dominated by snapping shrimp, sea urchins, fishes and other reef animals, normally increases in intensity after sunset coinciding with when pueruli are actively swimming in the water column (Booth, 2001; Cato and McCauley, 2002; Radford et al., 2010). Pueruli of spiny lobsters have arrays of pinnate sensory setae along the antennae that may provide the capacity for sound detection (Phillips and Macmillan, 1987; Macmillan et al., 1992; Jeffs et al., 1997; Jeffs et al., 2005; Montgomery et al., 2006). No behavioural experiments demonstrating active orientation to underwater sound have been reported in *J. edwardsii* or any other spiny lobster species. However, underwater sound was implicated as a possible cause for more than 4,000

pueruli caught in the seawater intake of a power station on the west coast of New Zealand (Booth, 1989; Jeffs et al., 2005), and recently underwater sound from reefs was found to advance the physiological development of pueruli to juveniles (Stanley et al., 2015). The aim of this study was to determine the *in situ* orientation response of swimming puerulus of *J. edwardsii* exposed to underwater sound from a natural reef.

4.3 Materials and Methods

The directional swimming behaviour of pueruli of *J. edwardsii* in response to an ambient underwater reef sound was conducted in a field experiment in a sandy lagoon that was protected from waves at Castle Point, New Zealand (40° 54.2' S; 176° 13.8' E) (Figure 4.1). This experiment was performed on days around the new moon over the austral summers of 2013 and 2015 (7-10 February and 20-23 January, respectively). No specific permissions were required for this location and activity, as it did not involve endangered or protected species. Pueruli were collected using 24 crevice collectors deployed randomly in ~1-2 m water depth during low tide. The crevice collectors are described and illustrated in Booth & Tarring (1986) and consist of angled plywood sheets that mimic natural rocky crevice habitat. The collectors were left in running filtered sea water for three weeks before the experiment to leach out any residual chemicals from the plywood used in their construction. Collectors were emptied daily at low tide during daylight hours when pueruli are inactive and hiding in benthic crevices (Booth, 2001). To empty a collector a mesh bag was placed around the collector and carried to the shore where pueruli were removed and sorted into different stages following the schema of Booth (Booth, 2001). Collectors were immediately returned back into position in readiness for collection of pueruli during the following night. Only stage one pueruli were retained and used for experimentation as they were most likely to have arrived in the collectors in the preceding

hours of darkness from their pelagic migration. Regardless, stage one pueruli taken from collectors are known to continue actively searching at night for suitable habitat to complete their settlement (Booth, 2001; Hayakawa and Nishida, 2002). Collected stage one pueruli were held individually in 40 ml floating jars with perforated lids within a 60 l drum with aerated seawater until they were used in the experiment later that day. At sunset, the pueruli were transported within a 20 l bucket to the experimental site for trials during the night (Figure 4.1).

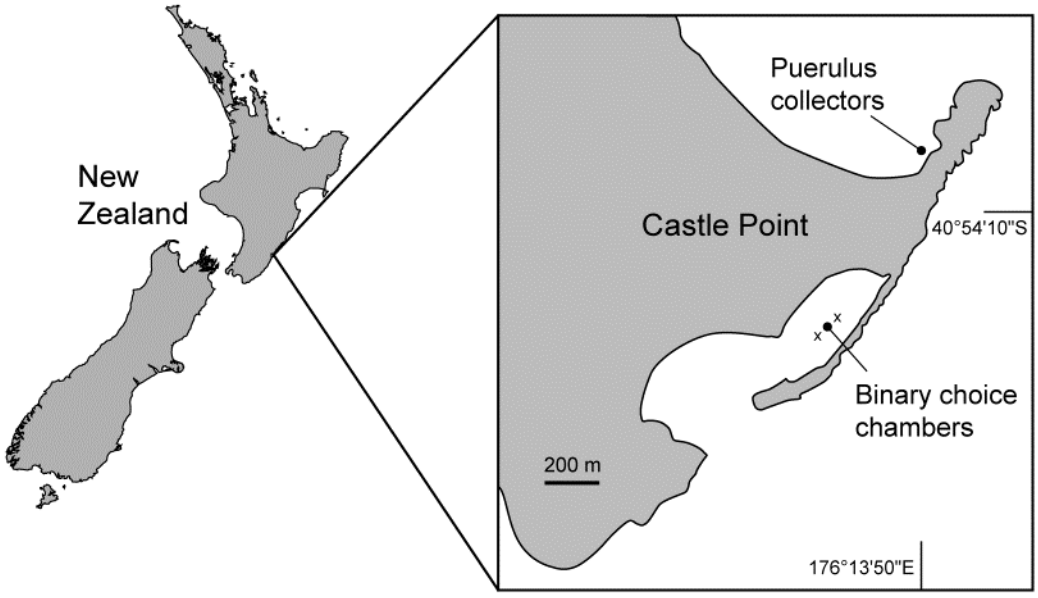


Figure 4.1. Castle Point experimental sites used for collection of pueruli and experimentation with behavioural choice chambers. "X" in the map represents positions of underwater speaker.

At the experimental site, replicate binary choice chambers were deployed in parallel at 2-3 m water depth and 1 m from the sandy seafloor (Figure 4.2A). Three to six replicate chambers were deployed depending on the number of pueruli obtained from the collections each day. The binary choice chambers were similar in design to that described by Radford et al. (Radford et al., 2007) and consisted of a transparent acrylic plastic tube (9 cm internal diameter, 100 cm long) with detachable trap ends (each 9 cm diameter, 15 cm long) covered with 500 μm plastic mesh (Figure 4.2B). A square frame made of transparent acrylic plastic sheet held three choice chambers spaced 20 cm apart. The choice chambers were oriented parallel to the rocky reef

running along one side of the lagoon to ensure there was no unequal influence of cues from reef habitat at either end of the choice chamber. An underwater audio speaker (Lubell Labs Inc., LL9642; 250 Hz–20 kHz, 170 dB re 1 μPa @ 1 m) was operated with a digital sound source (Sony MP3 player), an amplifier and a power supply housed inside a sealed drum floating above the speaker (Figure 4.2A). This speaker system was positioned at ~20-30 m from the end of the choice chambers with the position alternated on either end of the choice chamber between nights to remove directional bias ("X" in Figure 4.1). The ambient underwater reef sounds used in the experiments were recorded in north-eastern New Zealand (36° 15' 58" S, 174° 47' 37" E) during the spring at dusk over two nights on a new moon, using a remote underwater recording system that consisted of a calibrated HTI-96-MIN omnidirectional hydrophone (High Tech Inc., flat frequency response over the range of 10 – 24,000 Hz) connected to a digital recorder (Edirol R09HR 24-bit recorder; sampling rate 48 kHz, Roland Corporation, Japan), contained in an underwater housing. The hydrophone was placed 1 m off the seafloor in 23–25 m of water, and 80 m away from the margin of the coastal fringing rocky reef. There were no anthropogenic sources of noise such as large vessels or recreational boats visible in the area at the time of recording. All recordings were conducted in near calm conditions (< 0.5 m wave height and < 2.6 m s^{-1} wind speed; Climate Station, Leigh Marine Laboratory) so sound was primarily biological in origin rather than from waves or wind. Three typical 2 min sound sequences from the original habitat recording were randomly selected from a total of two hours of recording taken from a coastal reef in northeastern New Zealand on two separate nights and transferred to a MP3 player and used for playback in the experiments (113.5 ± 0.7 dB re 1 μPa RMS average in the 100 – 24,000 Hz range, mean ± S.E.). Three different sound sequences were chosen and assigned randomly for use on any one of the 23 experimental runs of the choice chambers to avoid pseudoreplication that would have occurred by using an identical segment of the recording for all experiments (Kroodsma et al.,

2001). There was a consistent peak in the spectra of all sound sequences located at around 1.2 kHz, which Radford et al. (2008b) assigned to the feeding sounds produced by the sea urchin, *Evechinus chloroticus*, and also higher frequency pulses from the snaps of snapping shrimp (Figure 4.3) (Radford et al., 2008c; Stanley et al., 2010).

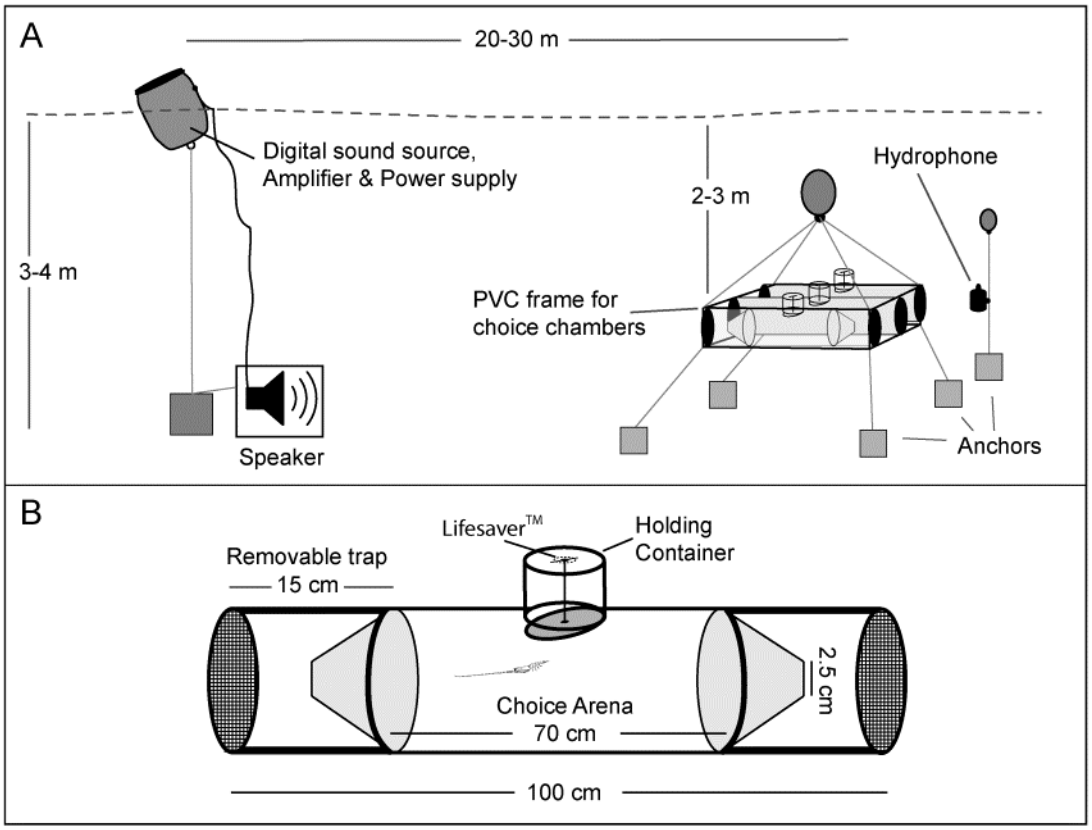


Figure 4.2. (A) Schematic of experimental set up, and (B) choice chamber design.

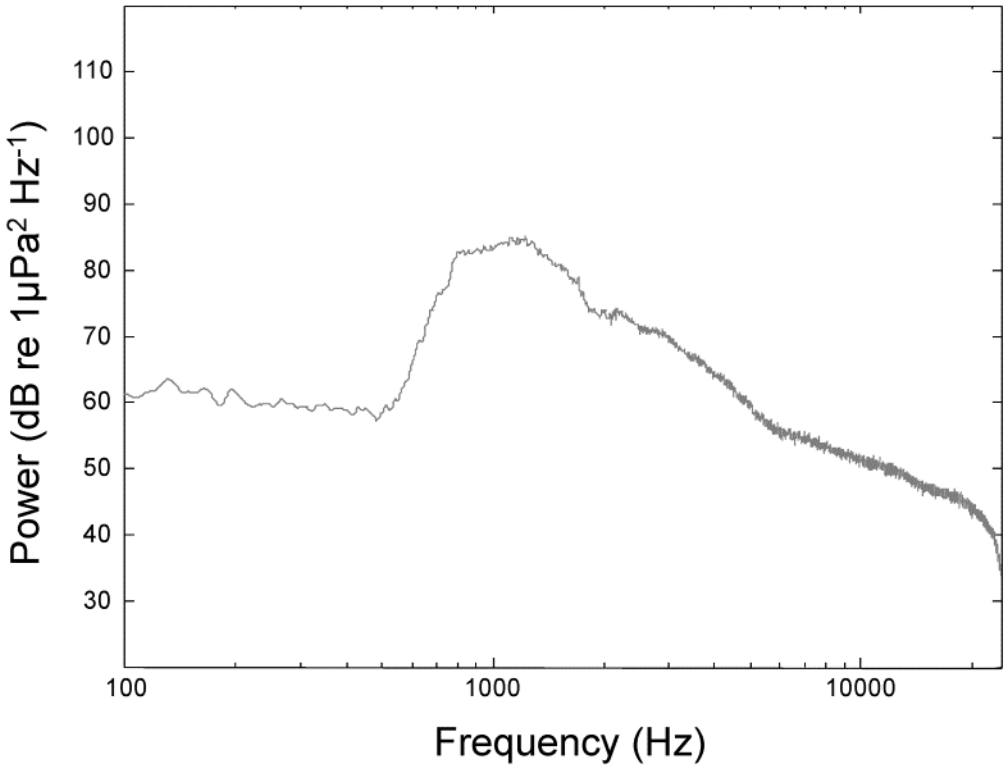


Figure 4.3. Power spectrum of ambient underwater reef sound recorded from a natural reef habitat of southern rock lobster in New Zealand. The power spectrum was generated using Fast Fourier transformation analysis of ten 10 s samples (100 – 24,000 Hz) randomly selected from the original recordings and smoothed using an 11 point triangular window using MATLAB software (MathWorks Inc.). Sound pressure levels were determined for between 100 – 24,000 Hz from each of the ten samples and the mean used for the experimental sound levels.

Deployment of pueruli into the chamber occurred during the night (21:00 to 01:00 hrs NZ Standard Time), whereby a single puerulus (n= 64) was transferred from the 40 ml floating jar to a sealed plastic holding container (400 ml). This container was then placed at the centre of the choice chamber by a diver on snorkel (Figure 4.2B). Both procedures were conducted with illumination by red light (Kodak Wratten Gelatin Filter #29; >600 nm) which is outside the visible spectrum of spiny lobsters (Weiss et al., 2006). Each puerulus was remotely released into the choice arena after approximately 20 min, by the automatic opening of the holding container as a result of a dissolving sugar lolly (Lifesaver^{TM}; Figure 4.2B). The choice chamber was surveyed one hour after attaching the holding container, leaving each puerulus ~40 min to make a directional choice by swimming into one of the traps at either end of the tube (Figure

4.2B). This time period was selected based on preliminary laboratory experiments that had indicated that the pueruli made a choice at around 30 min after release. The position of pueruli in the choice chamber (reef sound or silent side of the chamber relative to the speaker position) was recorded either *in situ* by a diver on snorkel, or by removing the chamber from the frame and observing in which end of the chamber the puerulus was trapped.

Underwater sound was recorded only during the 2015 experimentation with a calibrated remote hydrophone (SoundTrap 202, working frequency range of 0.020-60 kHz) that was located 1 m perpendicular to the choice chambers. This recorded the potential variation in ambient and replayed sound at the experimental site. The experiment was conducted under different wind speed and tide conditions (ambient conditions) on individual nights, and differences in choices under these conditions were analysed using a logistic regression model (Quinn and Keough, 2002). Corresponding tide phases were extracted from Meteorological Service of New Zealand's tide tables (http://www.metservice.com/) and the wind data from the National Climate Database (http://cliflo.niwa.co.nz/). The logistic regression models measured the relationship between a dichotomous categorical dependent variable (puerulus choice) and independent variables that could be continuous and/or categorical (ambient conditions) by using probability scores as predicted values of the dependent variable (Quinn and Keough, 2002). We included as independent variables: the speaker position ("north" or "south", relative to the chambers; "X" in Figure 4.1), the tide phases (as "stable" and "changing"), the wind gust direction, and the wind gust speed. The tide phases were included in the analysis to account for any influence of tide current on the swimming direction of the puerulus. The current was considered to be "stable" when experiments were conducted during low or high tides and "changing" when the tide was shifting between low and high. The model was run using a backwards step-down with a bootstrap of 1,000 iterations to determine which independent variables to include in the final model (Quinn and Keough, 2002; Harrell, 2015). These

analyses were performed using R using the regression modelling strategies (rms) package (R Development Core Team, 2008; Harrell, 2015). Additionally, we tested whether the pueruli were attracted by the artificial source of reef sound during the windy (>25 m s^{-1}) and non-windy days with two simple goodness-of-fit tests using an equal preference for both sides of the choice chamber as the expected frequency (Quinn and Keough, 2002). The data were pooled from all nights and were considered as observed frequency in the test (Quinn and Keough, 2002).

4.4 Results

Of the 64 pueruli tested, 59 (92.2%) moved and were trapped into one of the two sides of the experimental chamber. The remaining five hid in the delayed release mechanism so were excluded from analyses. Overall, the majority of the pueruli (n = 35; 59.3%) moved from the choice arena towards the sound, independent of the speaker position (Wald Z = 0.1; P = 0.96), wind direction (Wald Z = 0.7; P = 0.47) or tide phases (Wald Z = 0.8; P = 0.44; Table 4.1 & 4.2), indicating a behavioural choice. However, this selection by puerulus was moderated by the wind gust speed (Wald Z = -2.4; P = 0.02; Table 4.2; Figure 4.4). Sixty nine percent (n = 29) of the pueruli moved toward the artificial source of reef sound when wind gusts were below 25 m s^{-1} (χ^2 = 6.1; P = 0.01; n = 42). In contrast, pueruli exhibited no significant preference for either side of the choice chamber (χ^2 = 1.5; P = 0.23; n = 17) when the wind gust speed was higher than 25 m s^{-1}.

Table 4.1. Directional choice of pueruli in the behavioural choice chamber (towards or away from the artificial sound), position of the speaker, and ambient environmental variables at the experimental site (timing of low tide, gust wind direction and speed).

Date	Toward Sound (%)	Away from Sound (%)	N	Speaker position	Low tide time	Gust Dir. (Deg)	Gust Speed (m s^{-1})
7/02/2013	75.0	25.0	8	N	21:28	245	8.8
9/02/2013	80.0	20.0	5	S	22:27	314	17
10/02/2013	57.1	42.9	7	N	0:01	30	11.8
12/02/2013	33.3	66.7	9	S	1:52	328	25.7
13/02/2013	37.5	62.5	8	N	3:35	323	27.8
20/01/2015	60.0	40.0	10	N	23:44	208	16.5
21/01/2015	33.3	66.7	3	S	0:26	162	10.8
22/01/2015	80.0	20.0	5	N	1:10	193	10.8
23/01/2015	100.0	0.0	4	S	2:00	40	7.7

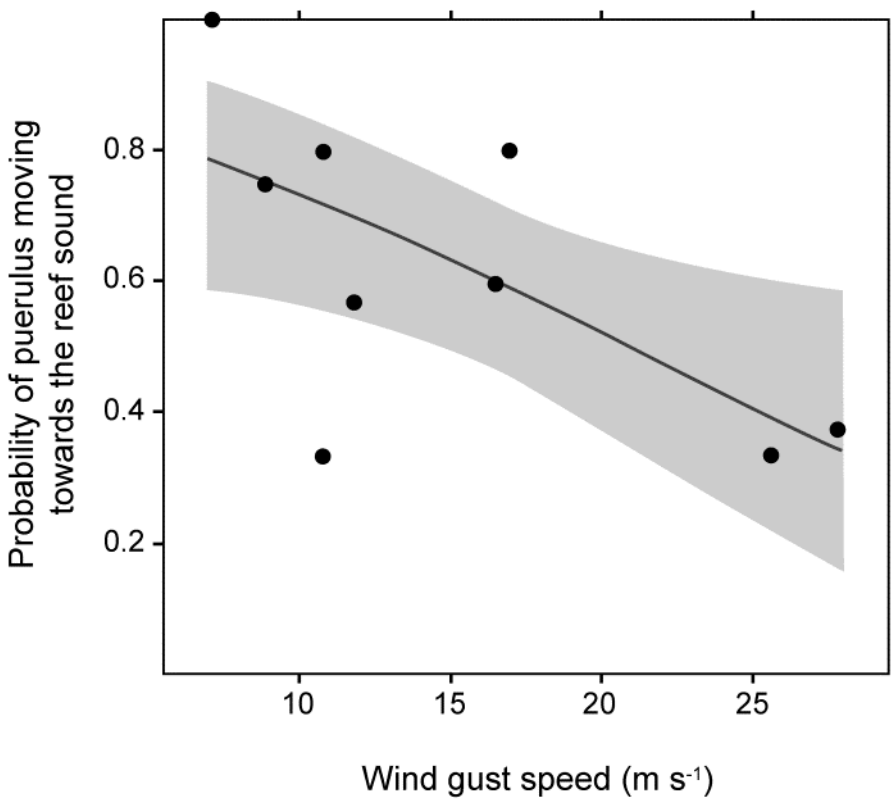


Figure 4.4. Predicted probability of puerulus choosing to move towards the reef sound moderated by the wind gust speed (m s^{-1}), based on a logistic regression (grey area represents the 90% CI). Black dots in the graph represent the observed proportion of the puerulus per night choosing to move towards the reef sound.

Table 4.2. Logistic regression of the directional choice of pueruli in relation to the speaker position and environmental variables (tide phase, wind gust direction and wind gust speed).

Model: Pueruli choice = intercept + speaker position + tide phase + wind gust direction + wind gust speed

	Coef.	S.E.	Wald-Z	Pr(>|Z|)
Intercept	1.7	0.8	2.2	0.031
Speaker position	0.0	0.6	0.1	0.956
Tide phase	0.5	0.6	0.8	0.440
Wind gust direction	0.0	0.0	0.7	0.465
Wind gust speed	-0.1	0.1	-2.1	**0.034**

Model validation: Backwards Step-down

Deleted	χ^2	d.f.	P	Residual	d.f.	P	AIC
Speaker position	0.0	1	0.956	0.0	1	0.956	-2.0
Wind gust direction	0.6	1	0.451	0.6	2	0.752	-3.4
Tide phase	0.3	1	0.561	0.9	3	0.823	-5.1

Suggested Model: Pueruli choice = intercept + wind gust speed

	Coef.	S.E.	Wald Z	Pr(>|Z|)
Intercept	1.959	0.733	2.670	0.008
Wind gust speed	-0.094	0.040	-2.370	**0.018**

Suggested Model Likelihood Ratio Test

LR (χ^2)	6.020
d.f.	1.000
P	**0.014**

The ambient underwater sound recorded at the choice chambers in the absence of replayed reef sound had a similar power spectrum among days, with higher acoustic power at lower frequencies (below 300 Hz) during the summer of 2015 (Figure 4.5A). In contrast, in the presence of replayed reef sound the sound recorded at the choice chamber had higher acoustic power overall and especially at frequencies around 1.2 kHz that were consistent with the overall sound intensity and spectrum of the reef from where the original recordings were taken (Figs. 4.3 & 4.5B).

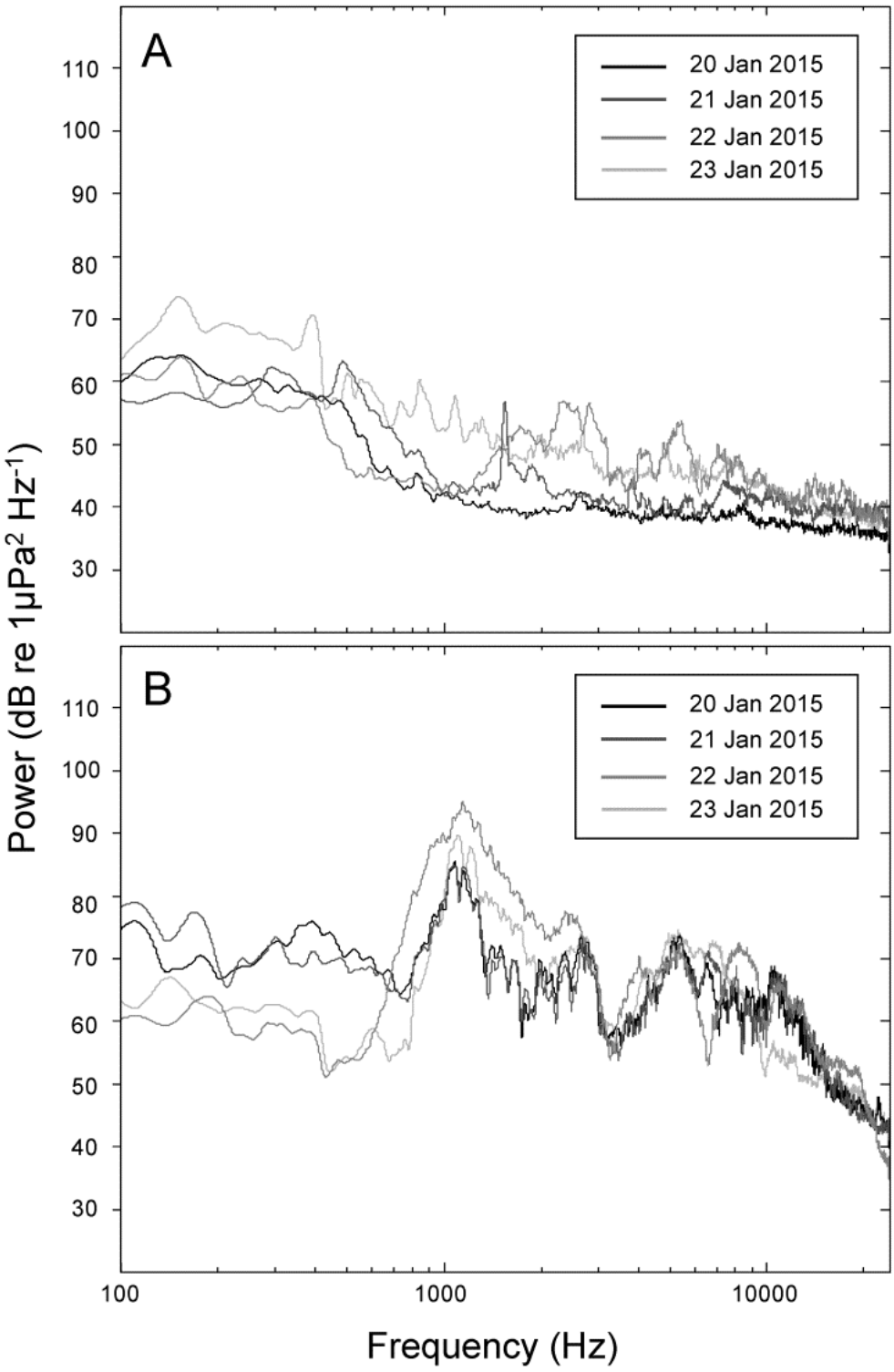


Figure 4.5. Power spectra of underwater sound recorded for each night at the experimental site in January 2015 (A) immediately prior to the artificial source of underwater sound commencing, and (B) during the experiments with the artificial source of underwater sound present.

4.5 Discussion

Pueruli of *J. edwardsii* actively moved toward the projected sound of a natural reef, suggesting that they could use reef sound as a cue to find reef habitats in which to settle. In the experiment pueruli made directional choices within the confines of a choice chamber within which there would have been a negligible sound pressure gradient, given that there is very little attenuation of sound propagated in seawater, especially at the lower frequencies that dominated the replayed reef noise (Knudsen et al., 1948). Therefore, it is most likely that the pueruli are sensing and responding to the directionality of the particle velocity component of sound rather than any pressure differential. Similar directional behavioural choices have been reported in the pelagic settlement stages of a wide range of coastal fishes, decapod crabs and coral (Jeffs et al., 2003; Simpson et al., 2005; Montgomery et al., 2006; Radford et al., 2007; Radford et al., 2008a; Simpson et al., 2008; Vermeij et al., 2010). In our experiment, higher wind velocity reduced the effect of the reef sound on swimming direction of pueruli. This is likely to be due to the increase in abiotic underwater sound at higher wind speed (e.g., >20 m s^{-1}) as a result of the disturbance of the sea surface or breaking waves on the nearby reefs (Knudsen et al., 1948; Cato and McCauley, 2002). This abiotic sound from wind would have partially overlapped the dominant bandwidth of our projected reef sound, i.e., 50 - 1100 Hz (Knudsen et al., 1948; Cato and McCauley, 2002). Scattered sources of increased sound from the surface of the water would have the potential to mask directional sound emanating from coastal reefs, making it more difficult for pueruli to detect from amongst the background sound (Cato and McCauley, 2002).

The distribution of the phyllosoma stages of *J. edwardsii* are mainly influenced by large scale transport processes, such as currents and eddies, where diurnal vertical migration may result in their retention 100's km from benthic populations (Chiswell and Booth, 1999; Booth and Ovenden, 2000). The phyllosoma metamorphose to the pueruli as far as 200 km offshore

from shallow coastal habitats (Jeffs et al., 2001a) and the pueruli have been observed rapidly swimming in straight lines at the sea surface at night (Jeffs and Holland, 2000). There is evidence that the movement of pueruli across the shelf can be influenced by large scale transport processes such as Ekman Current transport associated with along shore winds (Linnane et al., 2010b). However, active swimming by pueruli also appears to play an important role in onshore transport, possibly explaining why in some locations, such as Castle Point, New Zealand, it has not been possible to determine a relationship between puerulus settlement and local environmental variables that would otherwise be associated with passive onshore transport of larvae (Hayakawa et al., 1990).

Pueruli of *J. edwardsii* are a non-feeding (lecithotrophic) stage that depend only on the energy reserves stored during the preceding phyllosoma phase so the duration of the pueruli phase is constrained by these limited energy reserves (Jeffs et al., 1999; Fitzgibbon et al., 2014). Therefore, it seems unlikely that pueruli would rely solely on an orientation cue that is only available during calm conditions, and more likely use a hierarchy of orientation cues, as has been found in settlement stages of other species (Kingsford et al., 2002; Staaterman et al., 2012; Igulu et al., 2013). In windy conditions, pueruli may be able to use other shoreward cues for orientation such as celestial, hydrodynamic or chemical cues (Jeffs et al., 2005; Goldstein and Butler, 2009; Kough et al., 2014). For example, chemical cues derived from suitable settlement habitats were found to elicit a chemotactic response in the pueruli of *Panulirus argus* (Goldstein and Butler, 2009). Higher concentrations of pueruli of *P. cygnus* have been found at the surface of the sea in rough sea conditions, possibly using directional cues from waves, such as Stoke's drift (Phillips et al., 1978). Similarly, *in situ* experiments on tethered pueruli of *P. argus* found they were orientating in response to wind direction as well as tidal flow (Kough et al., 2014). Consequently, it is possible that *J. edwardsii* pueruli may use other directional cues at times when strong winds mask underwater sound orientation cues.

In most spiny lobster species the temporal and spatial pattern of settlement of pueruli is difficult to predict but it is important for estimating the future levels of recruitment to valuable fisheries for these species (Gardner et al., 2001; Booth and McKenzie, 2009; Kough et al., 2013). Therefore, an ability to determine the effectiveness of physical orientation cues used by pueruli, and to predict the migration pathway of the pueruli from metamorphosis to eventual settlement location, has the potential to improve the predictive power of biophysical models (Kough et al., 2013; Staaterman and Paris, 2014). This is likely to be important in spiny lobster because their pueruli have considerable capacity for active migration versus relying on passive transport or weak swimming capabilities alone. For example, the pueruli of *J. edwardsii* can swim at velocities around 10-40 cm s^{-1} for sustained periods providing the capacity to move considerable distances shoreward provided effective orientation cues are in use (Jeffs and Holland, 2000; Wilkin and Jeffs, 2011).

The experiment in the current study used only underwater sound previously recorded from a reef habitat in which *J. edwardsii* lobsters were present in north-eastern New Zealand (Radford et al., 2008c; Radford et al., 2010) suggesting that pueruli can detect sounds and be attracted by them in certain conditions. However, there is good evidence that differences in underwater sound associated with differences in habitat at their source may be used by pelagic settlement stages of other species to remotely select and orientate their migratory behaviour (Leis et al., 2002; Simpson et al., 2008; Radford et al., 2011a; Stanley et al., 2012). The research methods used here for pueruli of *J. edwardsii* could also be applied to test the effect of different sources of underwater sound or from the sound of different coastal settlement habitats. Additional research is also required to determine the range offshore over which the underwater sound may provide an effective orientation cue, including confirming the extent to which wind on the sea surface would mask the reliable detection of the sound cue (Stanley et al., 2011). Previous studies estimating the ranges at which larvae can detect underwater sound have tended

to use measures of sensitivity to sound pressure to estimate possible detection ranges, however, this may be inappropriate if, as the results of this study suggest, marine organisms are using particle velocities to detect sound directionality (Radford et al., 2011b). Improving our understanding of the effective range of underwater sound cues in lobster pueruli will therefore rely on determining both their sensitivity to the particle motion component of the acoustic field and the directional component of particle velocities of underwater reef noise at different distances from source.

A recent study has demonstrated that the development of settled pueruli of *J. edwardsii* to first instar juvenile was significantly advanced by exposure to underwater sound associated with their typical coastal settlement habitat (Stanley et al., 2015). This is consistent with the results of previous studies that have found that underwater sound associated with optimum settlement habitats not only provides an orientation cue for pelagic settlement stages of crustaceans, but also expedites physiological development, as well as eliciting behaviours associated with settlement, such as benthic exploration (Radford et al., 2007; Stanley et al., 2012).

In the megalopae of a number of crab species, the habitat type or quality influences settlement behaviour (Stanley et al., 2010; Stanley et al., 2012). Habitat type is also known to affect the survival of early benthic stage *J. edwardsii* and this could influence spatial patterns in abundance (Hinojosa et al., 2015). This is of particular interest with *J. edwardsii* because there have been recent dramatic changes in coastal reef communities across part of their range as a result of climate change and the removal of predators of sea urchins (Shears et al., 2008; Bates et al., 2014; Hobday and Pecl, 2014; Verges et al., 2014). Changes in these communities brings marked changes in the soundscape from the reefs (Radford et al., 2010; Radford et al., 2014; Nedelec et al., 2015) and potentially may have some major impacts on the orientation and settlement of the pueruli of *J. edwardsii* as occur in other species (Leis et al., 2002;

Simpson et al., 2008; Stanley et al., 2012). For example, the dramatic loss of kelp from reefs and replacement with urchin-dominated barren reef habitat has been associated with very marked differences in the frequency and intensity of the corresponding underwater sounds these different habitats produce (Radford et al., 2010). These changes in the important underwater sound cues used by settling pueruli have the potential to greatly influence the successful settlement and recruitment in this spiny lobster species.

Overall, the settlement of *J. edwardsii* appears to involve active nocturnal searching (Booth, 2001) where multiple cues from the habitat may be involved to guide the pueruli to reef so that they can locate a hole or crevice in which to settle (Jeffs et al., 2005; Hinojosa et al., 2015) . Underwater sounds can be detected tens of kilometres offshore (Kingsford et al., 2002; Radford et al., 2011b; Nedelec et al., 2015) so it is feasible that sound could be used by pueruli to orientate their swimming after metamorphosis from the phyllosoma. However, the distance at which this cue may be used by pueruli needs more empirical research. Our experiment demonstrated that pueruli, under certain conditions, can respond to the directionality of underwater sound suggesting that sound can play a role in successful settlement and survival of this valuable species.

4.6 Acknowledgments

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Chapter 5: Settlement and early survival of southern rock lobster, *Jasus edwardsii*, under climate-driven decline of kelp habitats

This work has been published as:

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Crevice collector used to monitor settlement of *Jasus edwardsii* with natural giant kelp, *Macrocystis pyrifera*.

"The number of living creatures of all Orders, whose existence intimately depends on the kelp, is wonderful… I can only compare these great aquatic forests of the southern hemisphere with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp…"

Charles R. Darwin in Patagonian Fjords (1913).

5.1 Abstract

Kelp habitats provide food, refuge, and enhance the recruitment of commercially important marine invertebrates. The southern rock lobster, *Jasus edwardsii*, supports valuable fisheries in southern Australia and New Zealand. Kelp habitats once covered large areas of inshore reef around Tasmania, Australia, but coverage has reduced over the last few decades due to climate change, especially off the eastern coast of the island. We investigated whether the kelp influences the settlement of lobster post-larvae to artificial collectors and how the presence of kelp affected the overnight predation on the early benthic phase (EBP). Settlement of lobster was tracked over six months using crevice collectors that had either natural or artificial giant kelp, *Macrocystis pyrifera*, attached, or nothing attached (control). Collectors with natural kelp had higher catches than those with artificial kelp or controls ($P = 0.003$), which suggested enhanced settlement through chemical attraction. Additionally, we measured overnight predation of the EBP in barren and kelp habitats individually tethered to artificial shelters. The kelp habitat was dominated by brown macroalgal species of *Ecklonia radiata*, *Phyllospora comosa* and *Macrocystis pyrifera*, while the barren was devoid of macroalgae. Survival of the EBP was higher (~40%) in the kelp habitat than the barren habitat (~10%) due to differences in predation ($P = 0.016$). These results suggest that the kelp habitat improves the recruitment of *J. edwardsii* and that decline in this habitat may affect local lobster productivity along the east coast of Tasmania.

5.2 Introduction

The availability of suitable habitats for settlement in coastal waters can be a bottleneck in recruitment of important fisheries species (Wahle and Steneck, 1991; Sheaves et al., 2014). On temperate marine reefs, the loss of productive kelp forest is one of the most dramatic ecosystem shifts reported (Filbee-Dexter and Scheibling, 2014). This ecosystem change affects local species diversity, produces changes in food webs, reduces available habitat for small organisms, and can also have localised impacts on the productivity of important fishery resources (Byrnes et al., 2011; Harley et al., 2012).

The southern rock lobster, *Jasus edwardsii*, supports valuable fisheries in southern Australia and in New Zealand. Females release between 50,000 and 500,000 larvae per year (Green et al., 2009), which spend 18 to 24 months as phyllosoma stages and are widely dispersed by ocean currents (Booth and Phillips, 1994; Bruce et al., 2007). The final stage phyllosoma metamorphose to a puerulus (post-larva), which can actively migrate into the coastal habitat (Jeffs et al., 2005). The mechanism by which the pueruli move inshore to settle is unclear, but it is thought to involve a combination of natural onshore advection and active onshore migration (Jeffs et al., 2005; Linnane et al., 2010b). Puerulus monitoring of *J. edwardsii* on artificial collectors has been undertaken across their distribution range for 30-40 years and their settlement trends have been correlated with the fishable biomass in some specific regions (Gardner et al., 2001; Linnane et al., 2010a; Linnane et al., 2014; Booth and McKenzie, 2009). The first few days immediately post-settlement in *J. edwardsii* (early benthic phase, EBP) is a period of high mortality due to predation by fish, octopus, crabs and other lobsters (Edmunds, 1995; Mills et al., 2006; Mills et al., 2008). Therefore, the availability of suitable habitats and shelters for EBP during this time could greatly affect their survival and recruitment, as occurs in other lobster species (Butler et al., 2006).

South-eastern Australia is one of the fastest warming coastal areas in the Southern Hemisphere, warming 3-4 times faster than the global average (Hobday and Pecl, 2014). An intensification of the South Pacific Gyre has been suggested as the main cause (Ridgway, 2007), where the warm and nutrient poor East Australian Current (EAC) is extending further south towards the eastern Tasmanian coast (Figure 5.1) (Johnson et al., 2011). The intensification of the EAC to Tasmania has resulted in the southward range extension of some marine species as well as benthic habitat changes, such as the depletion of kelp habitats and changes in their algal composition (Johnson et al., 2011).

Beds of giant kelp, *Macrocystis pyrifera*, off eastern Tasmania were once extensive enough to be harvested commercially (Sanderson, 1987), but have declined dramatically over the last 30 years (Figure 5.1; Johnson et al., 2011). This decline in giant kelp is believed to have been caused by the increasing influence of the EAC with nutrient-poor and warm waters (Johnson et al., 2011). Kelp habitats on reefs of eastern Tasmania have also been affected by grazing of the Australian longspine sea urchin, *Centrostephanus rodgersii*, which has extended its range southward as the EAC has strengthened (Ling et al., 2009). This range extension is the result of pulses of larval input from populations to the north of Tasmania over the past 30 years (Ling, 2008; Johnson et al., 2011). At high density, *C. rodgersii* overgrazes the productive macroalgal habitat, including reef previously dominated by *M. pyrifera*, so that areas of bare rock reef are created which are known as barrens habitat (e.g. Flukes et al., 2012). In northeast Tasmania these urchin barrens can cover 50% of nearshore rocky reef, although the barrens are not occurring yet towards the south or on the west coast of Tasmania (Johnson et al., 2011). In north-eastern Tasmania there is also a negative relationship between the abundance of the urchin, *C. rodgersii*, and the abundance of the sub-adult lobsters of *J. edwardsii*, which is causing concerns for the potential impact of this habitat change on lobster productivity (Johnson et al., 2011).

The early benthic phases (EBP) of *J. edwardsii* actively search for food and shelter (horizontal holes and crevices) in rocky reef at night when they are active (Butler et al., 1999; Booth, 2001; Hayakawa and Nishida, 2002). Also, the EBP eat small invertebrates that commonly inhabit marine vegetation (Edmunds, 1995; Mills et al., 2006). In this context, kelp also could offer protection from predation during periods of nocturnal activity, as well as a potential source of food because of their associated fauna. However, the relative importance of kelp habitat depletion on the recruitment of *J. edwardsii* has not been tested. Here we examine if the giant kelp attracts settling pueruli and whether the kelp habitat offers protection from predation during the nocturnal activity of EBP.

5.3 Methods

We undertook two field experiments to examine the importance of the kelp habitat on settlement and nocturnal predation of southern rock lobster, *Jasus edwardsii*. The first experiment tested whether the presence of giant kelp, *Macrocystis pyrifera*, influences settlement of pueruli. The second experiment compared the overnight survival of the early benthic phases (EBP) in a habitat with kelp species (i.e., *Ecklonia radiata* plus *Phyllospora comosa* and *M. pyrifera*) contrasted to a habitat that was barren of all macroalgal species due to overgrazing by urchins.

Giant kelp and *Jasus edwardsii* settlement – experiment design

To evaluate whether giant kelp, *M. pyrifera*, attracts pueruli of *Jasus edwardsii* we conducted an experiment on settlement onto crevice collectors at Bicheno (41° 52.3' S; 148° 18.1' E) (Figure 5.1). The crevice collectors were similar in design to that described and illustrated by Booth and Tarring (1986) and are used in Australia for monthly pueruli

monitoring programs (e.g. Linnane et al., 2014). A total of 18 crevice collectors were used with three treatments: six with natural giant kelp attached - testing for visual, chemical and structural cues; six with artificial giant kelp (http://www.pangea.dk/) - testing for visual and structural cues; and six collectors with no attachments, as controls. The artificial kelp is used for large public aquariums. The fronds were made of an extruded polyethylene plastic and the stipes consisted in a mix of 50% of polyethylene and 50% ethylene vinyl acetate, both of food grade standard. The artificial kelp was created by computer scanning a natural *M. pyrifera* from California, USA, which was used for preparing the production moulds which replicated the structure and colour of the upper parts of the plant but not the holdfast. Two complete natural young sporophytes of giant kelp including their holdfasts, or two artificial giant kelp, were attached onto each collector using cable ties (two stipes per collector). Both natural and artificial kelp were ~150 cm long and were replaced every month by fresh natural kelp or conditioned artificial kelp. Artificial kelp was conditioned by leaving it for at least one month in an indoor tank with flow-through seawater.

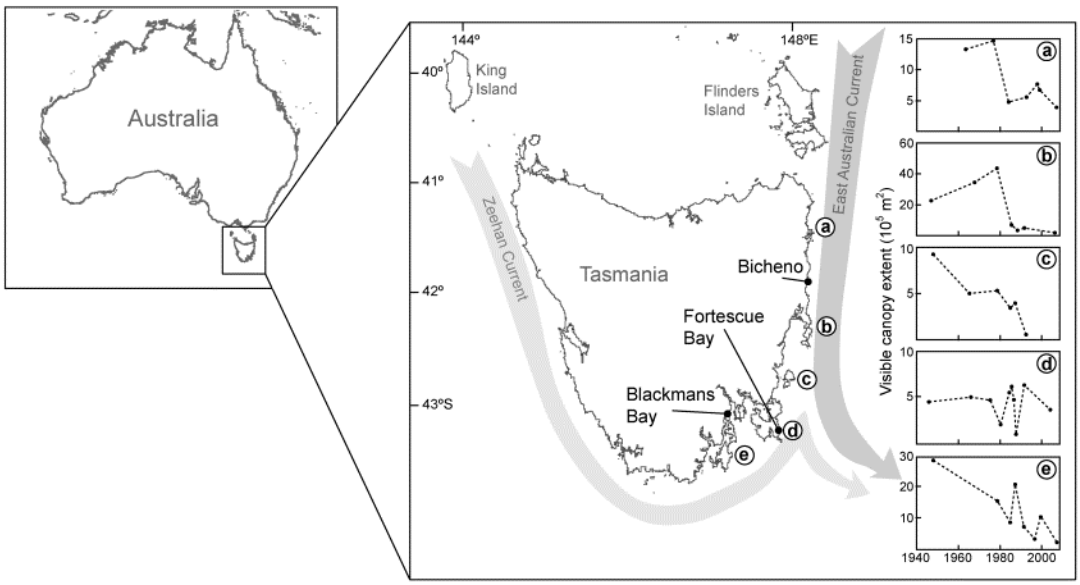

Figure 5.1. The main oceanographic currents around Tasmania (during winter when most settlement occurs) and the change in the extent of the visible surface canopy of *Macrocystis pyrifera* in five regions (a)–(e) on the east coast of Tasmania, 1940–2007. Bicheno and Fortescue Bay are the sites where the settlement and the predation experiments were done respectively. Oceanographic currents based on Cresswell (2000). Visible surface canopy of *M. pyrifera* as reported by Johnson *et al.* (2011).

Collectors were checked each month and kelp was replaced with new young sporophytes of giant kelp. These were removed using dive knives from natural reef at 3-5m depth via snorkelling at Blackmans Bay (43°0.5' S; 147°19.7' E; Figure 5.1). In the laboratory they were rinsed with seawater to remove epiphytes and grazers, and were maintained in running seawater for 15 to 20 h before to transport in a plastic drum with 80 l seawater to the experimental collectors at Bicheno.

Crevice collectors were arranged on a sandy bottom at 5 m depth in three parallel rows or lines (A, B and C) and six columns (Figure 5.2A). Each line (row) and column had the three treatments (natural kelp, artificial kelp, and control, Figure 5.2A). Two collectors with the same treatment were placed next to each other (3 m apart) in the same line. Collectors with different treatments were spaced 4 m apart (Figure 5.2A). The treatments on collectors were repositioned in a sequence by moving to the left each month after servicing to randomize any potential spatial effect from their position in the grid or from the individual collector (Figure 5.2A). This spatial design of three lines (A, B and C) and 6 collectors per treatment followed the guidance of Phillips *et al*. (2001; 2005), which controlled for the spatial effect on pueruli catches on collectors (i.e., corner and line effect). This included following the recommendation that at least two lines of collectors and at least twice that number of columns were required (see statistical analyses).

Pueruli catches were recorded from 16 July to 18 December 2013, commencing one month after the collectors and treatments were first installed (see Gardner et al., 2001). Collectors were serviced by divers who first placed a mesh bag around each collector including the kelp treatment. The collectors were then hauled to the surface for counting the catch of pueruli and EBP and to clean fouling. Each sample was conducted during the third week of the calendar month which was normally close to the full moon in this experiment. In a pilot experiment conducted in the previous year, the kelp (natural and artificial) attached to the

collectors and the collectors were sampled separately using individual mesh bags. No pueruli or EBP were found on kelp, or kelp holdfast, so sampling was simplified to include the kelp and the collector in the same bag.

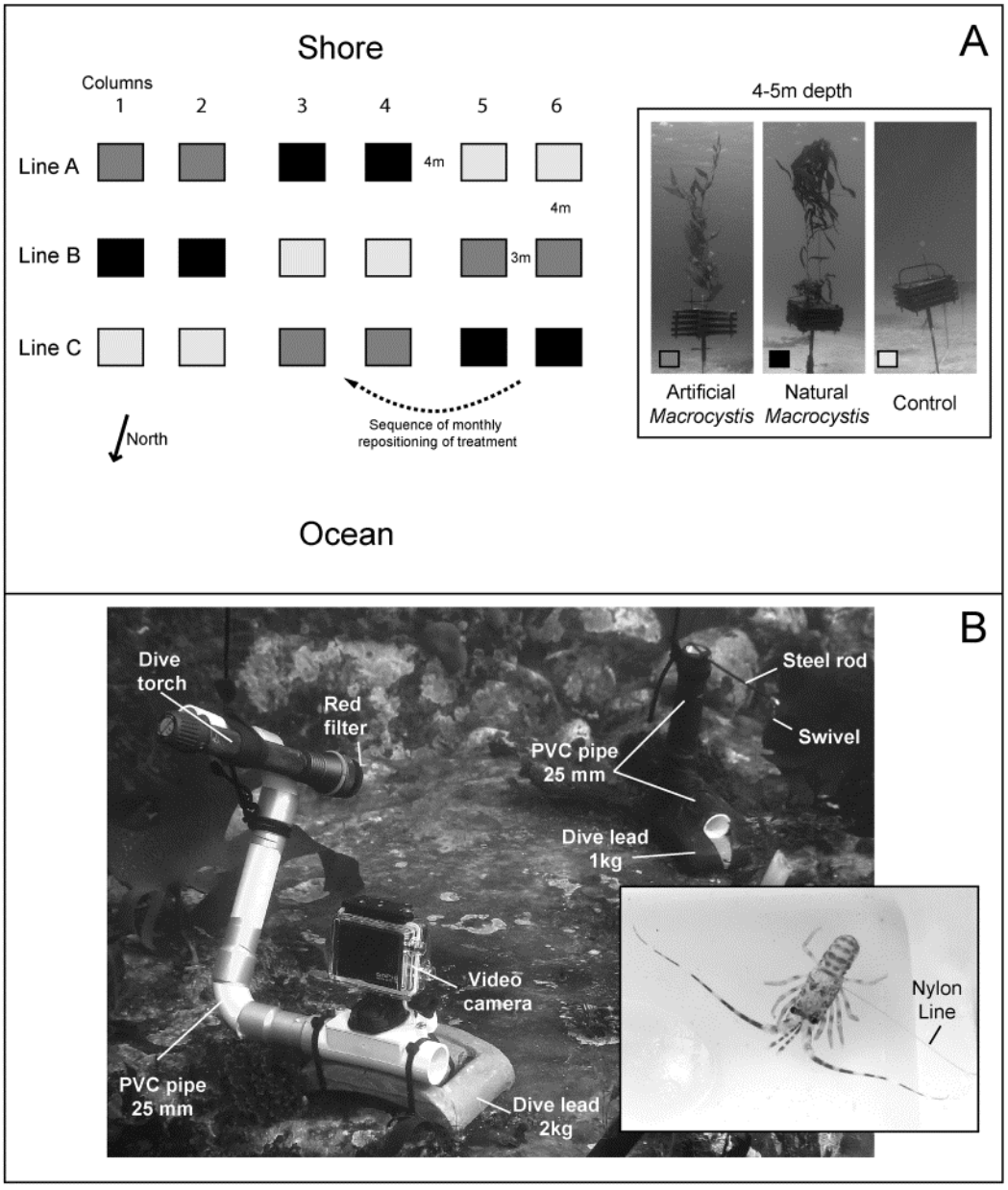

Figure 5.2. Schema of the experimental set-ups: A, arrays of crevice collectors at Bicheno used to examine the effect of *Macrocystis* (artificial and natural *Macrocystis*, and Control) on the catch rate of lobster (pueruli plus early stage juveniles). The collectors were arranged in three rows (collector lines) parallel to the shore line (A, B and C respectively) and in 6 columns. Each collector lines and column had 3 treatments respectively. The position of the treatments was repositioned each month to the left (as indicated by arrow). B, the camera system and artificial shelter used to evaluate the survival of the early benthic phase (EBP) at Fortescue Bay. Insert photo shows the EBP and the position of the monofilament tether.

Pueruli and EBP of different developmental stages were found on the collectors. The first three pueruli stages were categorised as S1 to S3, and the first and the second instar juveniles were categorised as J1 and J2 (or EBP) according to the schema of (Booth, 2001): S1s are completely clear pueruli (without any pigmentation on the body); S2s are clear but with a visible hepatopancreas (white); and S3s have pigmented exoskeletons. J1s and J2s occur after the moult from puerulus which is apparent by the change in morphology of the pleopods, which are shorter as they are no longer used for forward swimming. J1s and J2s are the first clearly benthic phase which are fully pigmented and the two categories were separated by size, as there is a moult between these stages (J2s >15 mm cephalothorax length).

Giant kelp and *Jasus edwardsii* settlement – statistical analyses

We primarily examined whether there were differences in lobster catches (pueruli and EBP) on collectors due to their spatial arrangement using three independent one way-ANOVA analyses (Figure 5.2A). These tests were performed to identify if spatial distribution of collectors could confound the statistical analysis of treatment. In these exploratory tests of spatial layout, catches were analysed independently of collector treatments and months, but these factors were included in the final analysis. ANOVAs treated the collector lines (A, B and C) and columns (1 to 6) as factors (Figure 5.2A). We also replicated the approach used by Phillips *et al*. (2001) to examine the "neighbour effect" with categories of collectors with two (corner collectors), three (collectors in the outer lines; Line A and C) and with four neighbours (i.e. collectors in line B). All data sets were transformed using log (x + 1), in order to achieve equal variances and normality from this count data.

As the number of lobsters on the collectors varied by line ($P = 0.002$), but not by column ($P = 0.663$), and the "neighbour effect" was not detected ($P = 0.135$) (Table 5.1) a Generalized Lineal Model (GLM) was used to evaluate differences in lobster catches among collector

treatments including collector line as a factor (see Randomized Block design in Quinn and Keough, 2002). The full GLM thus included factors of collector line (A, B and C), treatment (natural, artificial kelp and control) and month (July to December). ANOVA tests and GLM were conducted using R (R Development Core Team, 2008).

Table 5.1. Independent ANOVA analyses of the effect of collector orientation (columns and lines), and "neighbour effect" on *Jasus edwardsii* pueruli catch rate (replicates were a single monthly sample from a single collector). Lines (A, B and C), columns (1 to 6) and number of collector next to each other (2, 3 and 4) were considered as factors in two independent analyses. Line A was close to the shore and line C seaward (see Figure 2A).

Analysis	**Factors**						
ANOVA	Lines	Source of Variation	DF	SS	MS	F	P
data = log10(x+1)		Between Groups	2	1.004	0.502	6.349	**0.002**
		Residual	105	8.298	0.079		
		Total	107	9.302			
			Power = 0.050: 0.842				
		Tukey test	Diff Means	p	q	P	
		C vs. A	0.226	3	4.82	**0.003**	
		C vs. B	0.0533	3	1.137	0.702	
		B vs. A	0.173	3	3.683	**0.028**	
ANOVA	Columns	Source of Variation	DF	SS	MS	F	P
data = log10(x+1)		Between Groups	5	0.287	0.057	0.649	0.663
		Residual	102	9.015	0.088		
		Total	107	9.302			
			Power = 0.050: 0.050				
ANOVA	Neighbour	Source of Variation	DF	SS	MS	F	P
data = log10(x+1)		Between Groups	2	0.348	0.174	2.041	0.135
		Residual	105	8.954	0.085		
		Total	107	9.302			
			Power = 0.050: 0.218				

Differences among treatments and through time in the proportion of the different developmental stages of the pueruli encountered on the collectors was tested using two-way contingency tables to establish if the treatment may influence the timing of development of pueruli or their retention after settlement. One table considered the treatments on the collectors (natural and artificial kelp, and control) and pueruli stages (S1 to S3, and Juveniles) as

variables. In a second table, month (July to December) and puerulus stage (S1 to S3, and Juveniles) were considered as variables. The interactions between these variables were not considered in these analyses to simplify the results and interpretation. However, a graphical representation of all data is reported.

Kelp habitat and *Jasus edwardsii* early survival

Survival rate of the early benthic phases (EBP) of *Jasus edwardsii* was compared in kelp and in urchin barren habitats by tethering juveniles (J1) to artificial shelters located in both habitats. The experiment was done in August 2013 (Austral winter) at Fortescue Bay (43° 8.4' S; 147° 58.0' E; Figure 5.1) on rocky reef at 10 m depth. The kelp habitat was dominated by brown macroalgae species of; the common kelp, *Ecklonia radiata* (~70%); the crayweed, *Phyllospora comosa* (~20%); and the giant kelp, *Macrocystis pyrifera* (~10%), while the urchin barren was devoid of macroalgae.

Artificial shelters were used to standardize variation in natural crevice structure between habitats following Mislan and Babcock (2008), Mills *et al*. (2008) and Weiss *et al*. (2008) designs. The artificial shelters were constructed with two PVC tubes of 25 mm diameter and a PVC elbow to form an “L” shape with a base of 75 mm length and a height of 120 mm (Figure 5.2B). The base tube was blocked inside with a plastic barrier to create a shelter of 25 mm diameter ×75 mm length, which was similar in size to holes used by EBP on natural substrate (Edmunds, 1995; Butler et al., 1999). The shelter was attached to a 1 kg dive lead with cable ties. A steel rod was attached to the top of the L-shaped pipe with a swivel at the tip and secured using electrical insulation tape. Electrical insulation tape was wrapped around the structure to cover any gaps that could otherwise be used by EBPs. All the artificial shelters were placed in a tank with running seawater for one month before use to enable surface fouling to develop.

Pueruli used for the experiment were collected in July 2013 from Bicheno using the crevice collectors and the method described above. The animals were transported in seawater in an 80 l plastic drum then maintained in a 400 l tank with flow-through seawater. After the pueruli reached the J1 stage they were fed with open mussels *ad libitum*. Only J1 stages were used in this experiment (n = 70; 11.05 ± 0.16 mm CL, mean ± SE).

Tethers were attached to the EBP using the method described in Mislan and Babcock (2008). A 250 mm long monofilament nylon line (0.25 mm diameter, 2.7 kg breaking strength) was tied to the cephalothorax of the EBP between the 4th and 5th pairs of periopods and fixed to the cephalothorax with a drop of cyanoacrylate glue (Figure 5.2B). This tether was then attached to the swivel on the rod at the top of the shelter. Tethering from the top of shelter allowed the EBP to move between the inside of the shelter and around the seafloor within a circular area of ~100 mm of radius.

EBP were attached to shelters in the laboratory at least 24 hrs before being transferred to the experimental site at Fortescue Bay in 70 l containers with seawater. Divers randomly placed the shelters with the EBP attached into the kelp and urchin barren habitats. The entrance to each shelter with the EBP inside was blocked with a piece of *E. radiata* during deployment and this was removed around 30 min before sunset at around 5:40 pm. Divers returned the following morning around 30 min after sunrise at around 6:45 am and recorded whether the EBP remained in the artificial shelter. Three runs of the experiment were conducted over three nights during one week. On the first night, 15 units were placed in each habitat treatment; on the second night 8 and 7 units were allocated to kelp and barren respectively; and on the third night 12 and 13 were allocated respectively.

Tethers clearly restrict the escape behaviour of the EBP so results do not provide an estimate of absolute survival but rather an indication of relative differences in survival between habitats. Bias in relative estimates from tethering can occur where a predation event occurs

through facilitation for an uncommon predator. This was evaluated previously in this species by Mills *et al*. (2008) who made special note of predation by crabs because they used the tether to "reel in" EBP so these events were excluded from their analyses. In these experiments we reduced the problem of predation by crabs through the overhead tethering design and also used video to observe predators as recommended by Mills *et al*. (2008). This was conducted using Go-Pro™ cameras quipped with extra battery capacity (www.gopro.com), and illuminated using a dive torch with a red filter (Figure 5.2B). The red filter was an INON red Filter LE or red cellophane paper. The cellophane filter was based on the Kodak Wratten Gelatin Filter #29 which transmits light at >600 nm, which is outside the visible spectrum of lobsters and octopus (e.g. Weiss et al., 2006). Cameras were set on time lapse and recorded every 5 s. Fourteen EBPs in the kelp habitat and 11 EBPs in the barren habitat were video monitored (03:26 ± 0:24 h × EBP^{-1} and 02:44 ± 00:23 h × EBP^{-1}, respectively, mean ± SE).

We tested whether the survival of the EBP was different between the two habitats with a simple goodness-of-fit test using an equal survival in both habitat as the expected frequency (Quinn and Keough, 2002). The data were pooled from the three sampling runs undertaken within the same week and were considered as the observed frequency in the test (Quinn and Keough, 2002). The effect of habitat type on the mean per cent of time that the EBP spent inside the shelter was determined with a t-test using data derived from analyses of video recordings, with each deployment providing a single sample and considering the total time of the video or when the EBP was predated. The proportional data was transformed taking the arcsine of the square root of the data (Zar, 2010).

5.4 Results

Effect of kelp on settlement

A total of 488 pueruli and EBP were caught within 18 crevice collectors over six months. The position of collector lines influenced the number of lobsters caught (P = 0.001, Table 5.2). Line A, that was closest to the coast caught significantly fewer lobsters (3.14 ± 0.45, mean ± SE) than the line B and C (4.94 ± 0.66; 5.47 ± 0.59; P < 0.05, Table 5.2). Treatment had an effect, with significantly higher numbers of lobsters on collectors with the natural kelp treatment (5.97 ± 0.64, mean ± SE) than the control collectors (3.47 ± 0.44; P = 0.004; Table 5.2 and Figure 5.3). The collectors with natural kelp also had more lobsters than the collectors with artificial kelp (4.11 ± 0.64; P = 0.033; Table 5.2). These patterns were consistent during time and there were no differences in catches among months (P = 0.180; Table 5.2 and Figure 5.4). Over the six months of sampling, 215 lobsters were caught in the collectors with natural kelp treatment (44%), 148 (30%) in artificial kelp, and 125 (26%) on the control collectors.

Table 5.2. Generalized Lineal Model on the number of lobsters per collector considering Months (Jul-Dec), Treatments (natural kelp - NAT, control of no kelp – CON, and artificial kelp - ART) and collector Lines (A-C) as factors.

Analysis	**Factors**						
GLM							
(quasi Poisson)	Months	Sourc. of Var	DF	Deviance	Df	Resid.	P
data =log10(x+1)	Treatments	NULL			107	19.105	
	Lines	Months	5	0.895	102	18.210	0.180
		Treatments	2	1.348	100	16.862	**0.003**
		Lines	2	1.591	98	15.271	**0.001**
		Linear Hypotheses:	Estimate	Std. Error	z value	Pr(>|z|)	
		NAT - CON	-0.317	0.100	-3.172	**0.004**	
		NAT - ART	0.244	0.098	2.498	**0.033**	
		CON - ART	-0.072	0.106	-0.687	0.771	

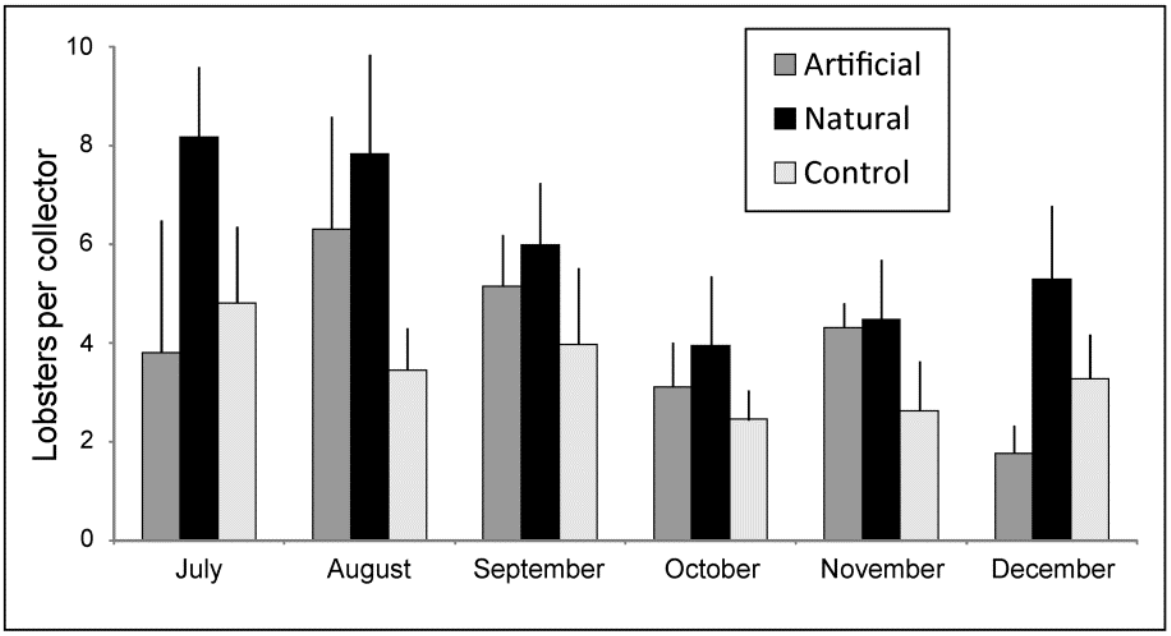

Figure 5.3. Mean (and standard error) of the number of *Jasus edwardsii* caught per collector treatment between July and December of 2013 (see Table 5.2 for statistical analysis).

Puerulus development stages on collectors

The development stage of pueruli was similar among treatments (χ^2 = 8.73; P = 0.189; Figure 5.4A & B), but different between sampling months (χ^2= 79.24; P < 0.001; Figure 5.4 A&B). This difference appeared to be mainly driven by changes in the proportion of the clear pueruli (S1) and juvenile lobsters (J1 and J2). Clear pueruli were absent in September and their proportion was higher in July and in November (Fig 4B). The proportion of juvenile lobsters was lower during July and much higher in September and October (Fig 4B).

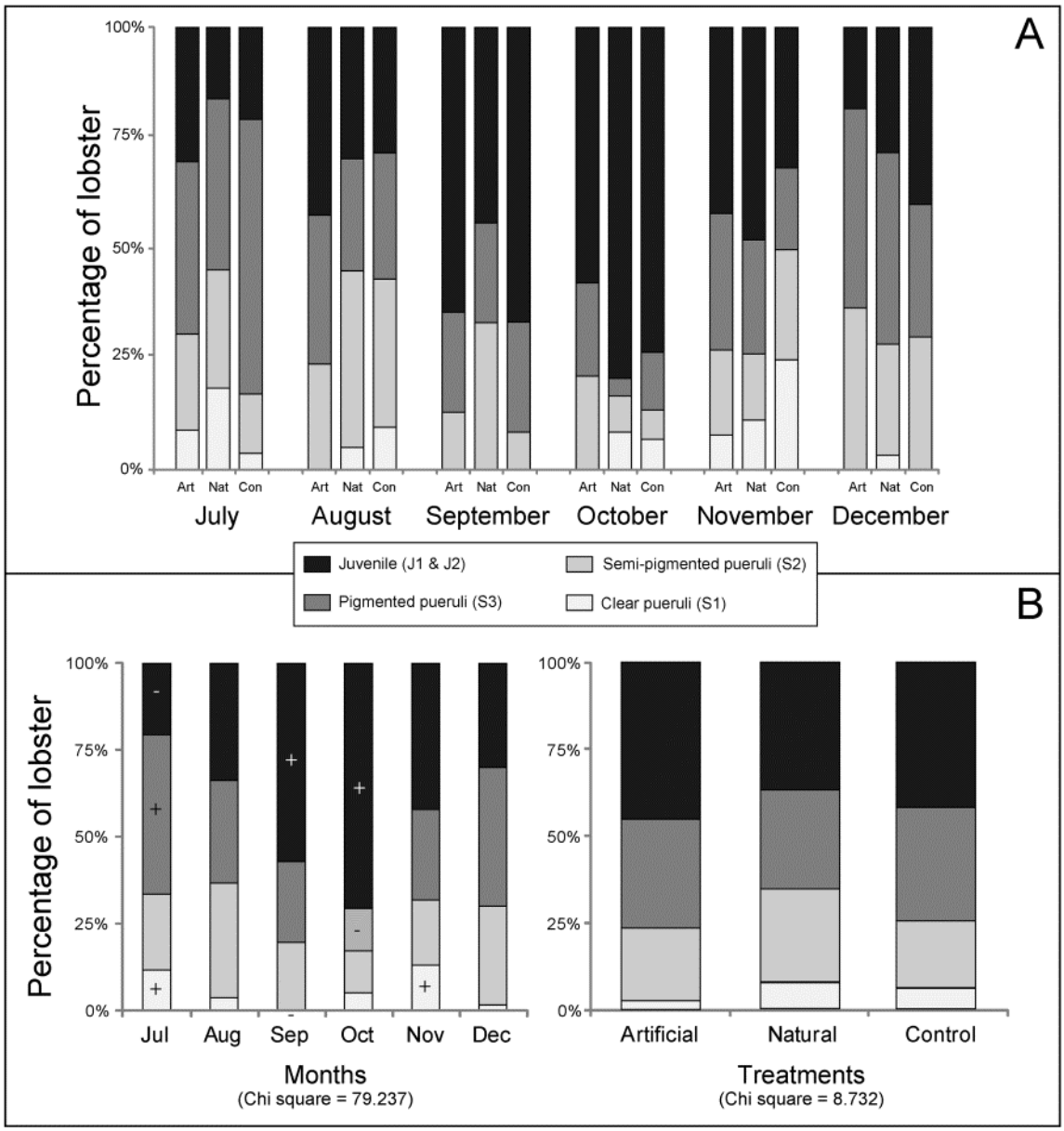

Figure 5.4. A, proportion of the different development stages of pueruli and juveniles of *Jasus edwardsii* collected between July and December of 2013 from three treatments on crevice collectors. B, contingency table results over months (critical value of Chi square (0.05, 15) = 25.0) and treatments (critical value of Chi square (0.05, 6) = 12.6). (+) and (-) represent the observed frequencies above and below the expected frequencies (Chi square values > 5, respectively).

Kelp forest and post settlement survival

Overnight survival of the EBP in this experiment was very low with less than 50% over each single night of the experiment. Tethered early benthic phases (EBP) had higher overnight survival in the kelp environment (42.9%) than in the urchin barren (11.4%) (χ^2 = 6.37; P = 0.016, Figure 5.5).

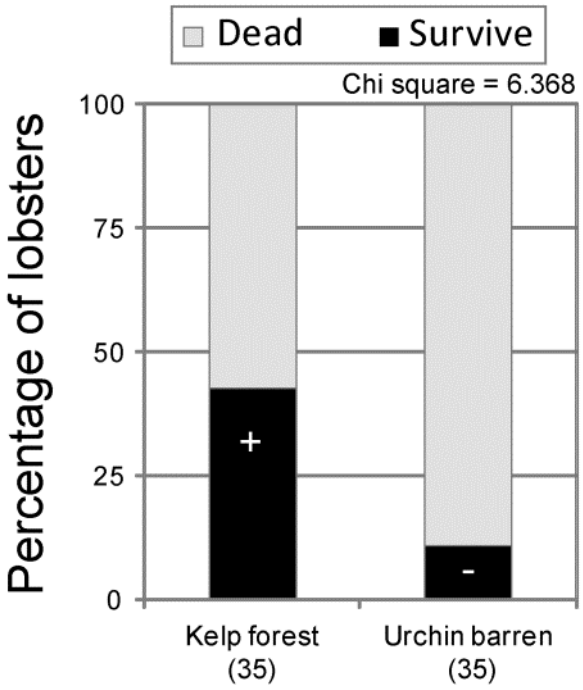

Figure 5.5. Proportion of tethered early benthic phase of *Jasus edwardsii* surviving in kelp and urchin barrens habitats. Numbers in parentheses are replicates. Critical value of Chi square (0.05, 1) = 3.8. (+) and (-) represent the observed frequencies above and below the expected frequencies (Chi square values > 3, respectively).

The shelter occupancy (proportion of time that the EBP spend inside the shelter) was similar between habitats (31.4 ± 10.6% in kelp habitat and 61.3 ± 14.1% in urchin barrens, mean ± SE)(t = -1.579; df= 23; P = 0.128). However, the statistical power of the analysis was 0.203, which was below the desired power of 0.800 (Cohen, 1988). Only one predator in the urchin barren was clearly identified from video recordings which was a rosy wrasse (*Pseudolabrus rubicundus*), with predation occurring before sunset. Non-lethal interactions with five fish species and two crab species with tethered EPB were recorded with pueruli successfully using the shelter to avoid predation (Table 5.3). From these non-lethal interactions, wrasse species appeared only in daylight, whereas the cod and the cardinal fish were more active during the night (Table 5.3). Additionally, when the EBP were stalked by fish species, they remained inside the shelter, and when the EBP were stalked by crab they escaped by a

quick backward swim response (Supplementary material, S1). A predation event by another labridae fish, the yellow-saddled wrasse (*Notolabrus fucicola*), was identified by the presence of the monofilament tether line and swivel in their mouth – this was observed by the diver rather than captured on video (Supplementary material, S2).

Table 5.3. Potential predators (predation risk) of the EBP of *Jasus edwardsii* recorded on video in kelp and urchin barren habitats.

	Scientific name	Common name	Recorded	Habitat	dark/daylight
Osteichthyes	*Notolabrus fusicola*	Yellow-saddled wrasse	1	Kelp	daylight
	Pictilabrus laticlavius	Senator wrasse	2	Kelp	daylight
	Meuschenia sp.	Leatherjacket	1	Kelp	daylight
	Pseudolabrus rubicundus	Rosy wrasse	1	Barren	daylight
	Vincentia sp.	Cardinal fish	1	Barren	dark
	Lotella rhacina	Beardie (cod)	2	Barren	dark
Decapoda	*Strigopagurus strigimanus*	Hermit crab	1	Barren	dark
	Plagusia chabrus	Speedy crab	2	Kelp & Barren	dark

5.5 Discussion

The results suggest that recruitment of *Jasus edwardsii* is enhanced in kelp habitat. Catches of the pueruli and early benthic phase (EBP) on collectors with the giant kelp *Macrocystis pyrifera* were higher than controls, suggesting that coverage of giant kelp on natural reef would attract pueruli to settle. Overnight survival of tethered EBP was also higher in kelp environment where an inherent quality that we have not identified, such as the structural complexity of this habitat, or differences in habitat-associated predators, reduced the predation events. Climate change induced loss of the kelp habitat would thus be expected to affect settlement and subsequent recruitment of lobsters to this valuable fishery (Johnson et al., 2011).

Settlement processes in *Jasus edwardsii*

The metamorphosis from phyllosoma to puerulus stage occurs far offshore from coastal reefs and has been detected beyond the continental shelf (Jeffs et al., 2001a). The mechanisms that pueruli use to return to coastal reef is poorly understood, but there is evidence that they orientate shoreward with long distance cues and active swimming in combination with physical transport (Jeffs et al., 2005; Linnane et al., 2010b). Pueruli of *J. edwardsii*, as other spiny lobsters, have sensory mechanisms that allow them to perceive and use multiple cues from their environment to guide their swimming including celestial, wind, acoustic and magnetic cues (Jeffs et al., 2005; Kough et al., 2014). Of particular interest for this study, laboratory experiments with *P. argus* showed that pueruli could identify coastal waters and would actively select these waters in choice experiments suggesting the use of chemical cues (Goldstein and Butler, 2009).

Once the pueruli of *J. edwardsii* reach coastal waters they may also use local cues to identify the settlement habitat, as do other several decapod crustacean species (Gebauer et al., 2003; Stanley et al., 2010). Observed higher pueruli settlement on collectors with the natural kelp, *M. pyrifera*, than collectors with plastic kelp and controls suggested that pueruli were receptive to chemical cues from the kelp, in addition to the physical structure of kelp. This local chemical attraction may guide the pueruli to locate a hole and/or crevice to settle, or attract them from surrounding habitats.

The time that the *J. edwardsii* puerulus (S1) takes to moult to juvenile (J1) has been estimated to be between 1-3 weeks depending on temperature (Booth and Stewart, 1993; Fitzgibbon et al., 2014), although, it could be affected by some chemical and physical cues from the habitat (Gebauer et al., 2003; Stanley et al., 2011). For example, reduction in the time to moult in pueruli of *P. argus* has been reported in response to the presence of chemical cues from the red macroalgae, *Laurencia* spp., which dominates their settlement habitat in Florida,

USA (Goldstein and Butler, 2009). If the giant kelp expedites the time to moult in *J. edwardsii* we could expect a difference in the proportion of the pueruli stages according with the treatments in our collectors. However, we did not find any difference of the pueruli stages among our collector treatments suggesting no effect on the time to moult within a monthly sampling.

Post-settlement predation on *Jasus edwardsii*

Structured habitats, such as seagrass beds, mangroves, corals, mussels and kelp can provide the necessary resources and environmental conditions to facilitate the settlement and survival of many other species including those of commercial importance (Grutter and Irving, 2007; Halpern et al., 2007; Almanza et al., 2012). For example, it is well established that mangroves enhance the settlement of some fish species where the two most important pressures governing this habitat selection are the risk of predation and the availability of food (e.g. Laegdsgaard and Johnson, 2001). In addition, direct predatory avoidance behaviour has been reported as an important driver to settle in some competent decapod larvae (Tapia-Lewin and Pardo, 2014). Our results suggest that kelp habitat may provide some predator protection, or there is a reduction of the potential predators for *J. edwardsii*.

The EBP of *J. edwardsii* inhabit small holes and crevices scaled to their body size, and forage only at night across small areas to reduce encounter rates with predators (Edmunds, 1995; Butler et al., 1999). Our experiment mimics nocturnal emergence and offered standardised artificial shelters similar to natural holes to avoid variation in this factor between kelp and urchin habitats. We found that the overnight predation of tethered EBP was lower in the kelp environment than in the urchin barren indicating that the kelp habitat reduces predation encounters possibly by obstructing prey detection and also changing the ability of predators to manoeuvre and capture prey (e.g. Syms and Jones, 2000; Rogers et al., 2014). This pattern of

reduced predation risk with increased structural complexity appears to be a general pattern observed in kelp habitats (Villegas et al., 2008; Kovalenko et al., 2012). The presence of kelp is also likely to increase the availability of food for juvenile lobsters (Caputi et al., 2013) and modify the predator composition and abundance (Pérez-Matus and Shima, 2010), although these factors were not directly examined in our experiments.

Climate changes and fishery implications in Tasmania

Our experiments confirm that settlement of *J. edwardsii* involves active searching (Booth, 2001) and that local settlement is increased by the presence of giant kelp. In addition, during the solitary and cryptic phase of EBP, kelp habitat reduced predation, possibly through modification of the suite of associated predators or their ability to successfully capture EBP. This facultative association between *J. edwardsii* and kelp habitats may "facilitate" (sensu Bruno et al., 2003) and enhance the recruitment in this lobster species.

Our results imply that climate change driven loss of kelp habitat may affect local productivity of the *J. edwardsii* fishery. There was a period of widespread declines in recruitment of *J. edwardsii* from 2004 to 2011, including in areas where the loss of kelp had occurred (Hartmann et al., 2013). Although this decline in recruitment occurred at a broader scale than the loss of kelp and was due to other processes (Linnane et al., 2010a), the impact of loss of kelp examined here could be expected to compound the effects of these low recruitment events. *Jasus edwardsii* recruit into a range of habitats where holes and crevices are available (Edmunds, 1995; Butler et al., 2006), however, the kelp habitat "facilitates" the recruitment process. *Jasus edwardsii* is possibly less vulnerable to a loss of kelp habitat than some other lobster species (Wahle and Steneck, 1992; Butler et al., 2006) because a change in kelp abundance would not be expected to create local extinction of the fishery but rather reduce productivity due to a reduction in recruitment.

Some quantification and future monitoring of the effect of habitat change may be possible in combination of data collected in puerulus settlement monitoring programs, which have been conducted across Australia and New Zealand since early 1990s (Gardner et al., 2001; Booth and McKenzie, 2009; Linnane et al., 2014). Change in survival of settling lobsters as a consequence of habitat change is expecting to affect the relationship between pueruli catch data from these artificial collectors and measures of future recruitment of adult lobsters to the fishery.

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Chapter 6: General Discussion and Conclusions

The research presented in this thesis investigates the mechanisms involved during the settlement process and post-settlement survival in *Jasus edwardsii* framed around three specific issues; 1) the effect of environmental variables on settlement, 2) the behavioural response of pueruli to environmental cues, and 3) the effect of habitat changes on coastal reefs along the east coast of Tasmania on the settlement and post-settlement survival of this important lobster species. The results presented in this thesis demonstrate that settlement is a complex process, involving the interaction of larger scale environmental variables in combination with local factors and larval behaviour. The results suggest that large scale environmental variables influence the synchrony in settlement at a regional scale (100-500's km), probably controlling the abundance and position of competent phyllosoma larvae, while the post-larvae appear to navigate onshore using a combination of orientation cues that include chemical and sound cues. Finally, reduction in kelp habitats on the east coast of Tasmania is expected to negatively affect local productivity of *J. edwardsii* due to a likely increase in predation.

6.1 Onshore advection

Data used in these analyses came from monitoring program of puerulus settlement for 17 years at 13 sites along the southern coast of Australia and New Zealand. Spatial synchronicity in the magnitude of settlement was observed at scales of around 100-500 km. Processes related to El Niño/La Niña events (SOI) and westerly storms and higher rainfall during winter/spring activity (DMI and SAM) appeared to influence this synchronicity. Higher rainfall and storm activity during winter/spring (negative DMI and SAM, respectively) and El Niño events (negative SOI) contributed to higher settlement in South Australia and Victoria

but led to lower settlement in Tasmanian sites. Similarly, during these climatic/ocean conditions in New Zealand, higher pueruli settlement occurred in the north-east of the South Island and in the south-east of the North Island (middle sites) but lower settlement in the southern sites. In contrast, in Tasmania and the southern sites of New Zealand, higher settlement was associated with weaker westerly winds and storm activity (positive DMI) and La Niña conditions (positive SOI). These analyses suggested that during El Niño events the south-westerly wind anomalies (Gordon, 1985; Cai et al., 2011) transport phyllosoma and pueruli to the north, whilst in contrast, during La Niña events the north-easterly wind anomalies might transport the pueruli further south in the whole study region (Figure 6.1). Anomalies in wind-driven sea surface currents and large-scale environmental processes have some influence not only on *J. edwardsii* settlement and could be a general pattern in spiny lobsters. For example, in the Caribbean spiny lobster, *Panulirus argus*, localised fluctuations in settlement have been correlated with hurricanes and associated sea level changes (Briones-Fourzan et al., 2008).

At Australian sites, variability in localised settlement of pueruli was correlated to some local environmental factors, such as wave period, wind strength and current transport direction, with sea surface temperatures being less important. However, an important proportion of the settlement variability was not explained by any of the environmental factors included in the models suggesting that other factors not examined here (e.g., fronts and/or eddy positions), or larval behaviour and their ecological interactions, may also be involved during their transport and settlement process (Chiswell and Booth, 1999; Phillips and McWilliam, 2009).

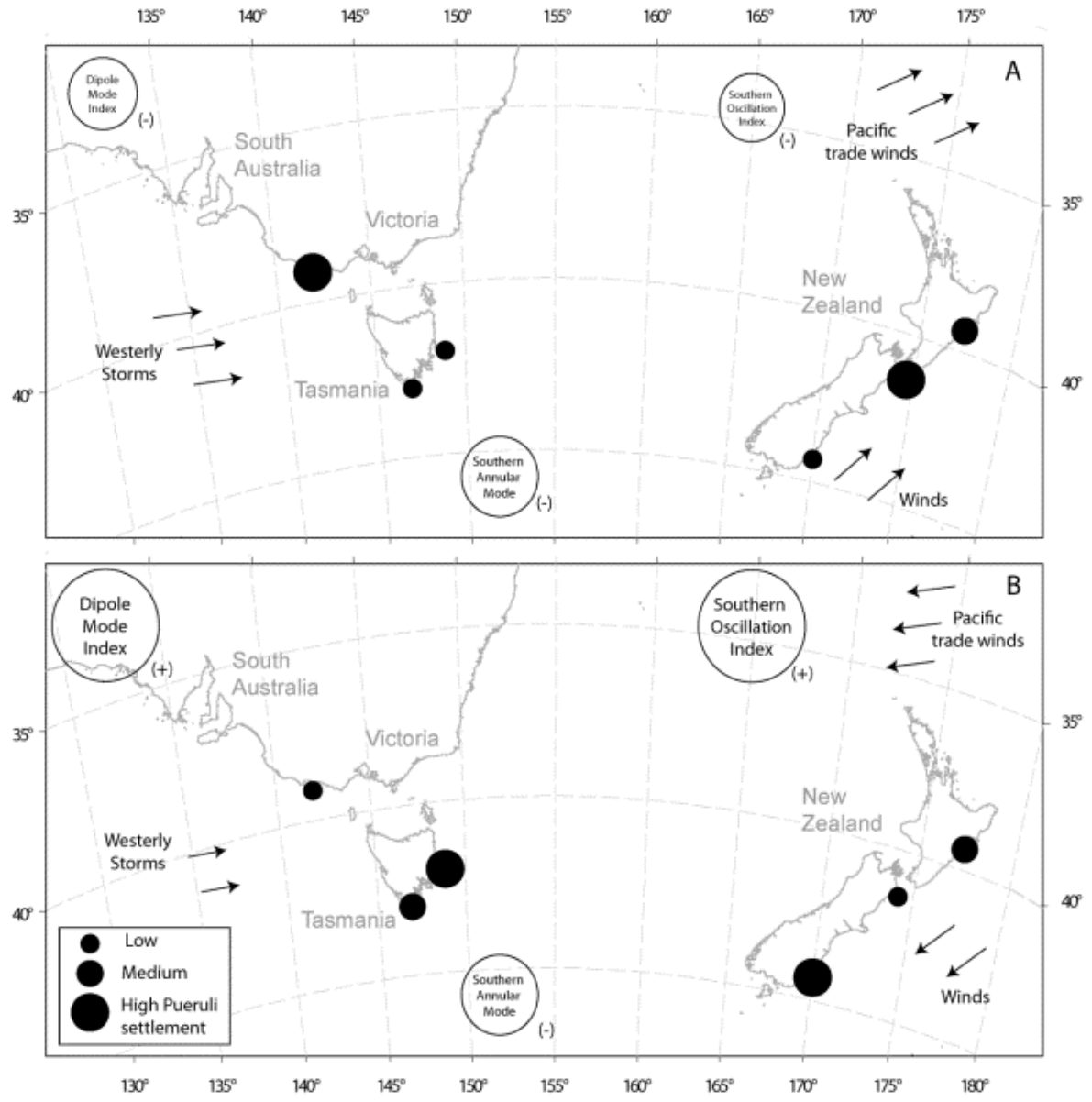


Figure 6.1. Conceptual model summarising large scale environmental index and settlement of *Jasus edwardsii* pueruli in southern Australia and New Zealand. A) Represents conditions of higher rainfall and storm activity during winter/spring (negative DMI and SAM, respectively) and El Niño events (negative SOI). B) Represent the opposite weather conditions; weaker westerlies and storm activity (positive DMI) and La Niña conditions (positive SOI).

6.2 Onshore orientation

Laboratory experiments showed that pueruli of *J. edwardsii* actively moved toward coastal waters when oceanic water was offered as an alternative choice, suggesting that pueruli may use chemical cues to orientate their onshore swimming. Kelp cues from *Macrocystis pyrifera* were also tested in the laboratory with stage I pueruli, but they were avoided by

pueruli. Also, *in situ* experiments conducted in New Zealand demonstrated that pueruli actively moved toward sound of a natural reef at wind intensities < 20 m s^{-1}, suggesting the use of reef sound by pueruli as a cue to find reef habitats in which to settle in certain weather conditions. These two results contribute evidence on the use of chemical cues and reef sounds, in combination with other cues, to find settlement habitat (Jeffs et al., 2005). For example, in situ observations of pueruli of the Caribbean spiny lobster, demonstrated that they adjusted their swimming orientation towards the coast in response to the tidal phase, possibly by making use of multiple orientation cues, such as celestial, wind, acoustic and magnetic cues (Kough et al., 2014).

Chemical cues emanating from the coastal habitats are typically transported several kilometres offshore before dissipating, generating a large scale concentration gradient, but how marine organisms might use these chemical cues for orientation are uncertain (Figure 6.2; Atema et al., 2012). Therefore, larvae migrating onshore may respond to chemical cues by switching to reef sounds, or another directional cue, once reaching closer proximity to coastal habitats as have been suggested for some fish species (Huijbers et al., 2012; Paris et al., 2013; Staaterman and Paris, 2014). Underwater sound has also the potential to be transmitted 10's km offshore where it could provide a directional cue for larvae (Radford et al., 2011b). The results of the behavioural experiment using sound suggests it is most likely that the pueruli are sensing and responding to the directionality of the particle velocity component of the underwater sound rather than any pressure differentials which imply their distance of potential detection. The distance at which these cues (chemical and reef sound) may be used by pueruli needs more empirical research. However, based on our results a theoretical model of shifting cues can be proposed (Figure 6.2).

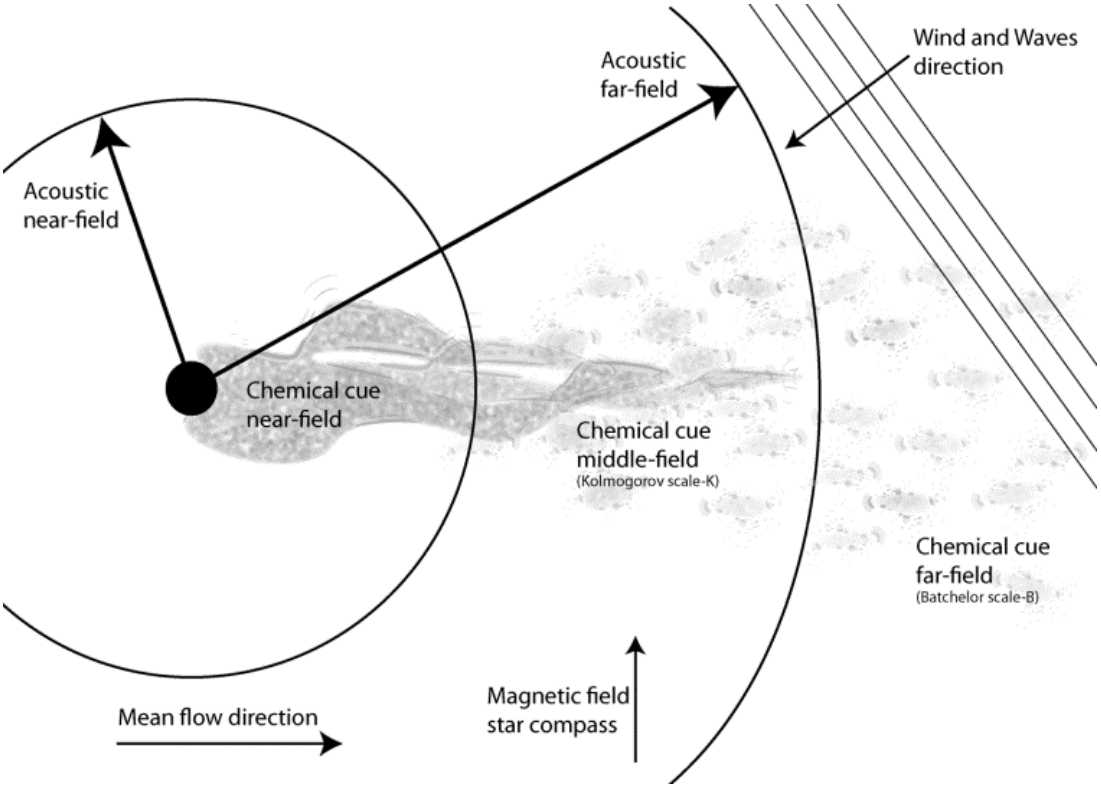


Figure 6.2. Theoretical simplistic model summarising cues and propagation available to pueruli for directional orientation allowing them to swim onshore toward a coastal reef (black circle). From far from the reef, pueruli orientation, or transport, is limited to the use of directional cues derived from wind and waves until some chemical cues become available (Batchelor scale, see Atema et al., 2012). At this distance from the reef (chemical cue far-field) chemical cues do not provide directional information due to the patchy condition of the propagation, but it could trigger the use of another cue such as acoustic cues. As they move further into the acoustic fields, chemical cues might be stronger (Kolmogorov scale) providing information about the source of the odour. Inside the acoustic fields pueruli may detect the direction of the sound source. Magnetic field and star compass are available during all this orientation process and they could be in use, but require empirical examination (adapted from Atema et al., 2012; Staaterman and Paris, 2014).

Pueruli are a non-feeding (lecithotrophic) stage that depends only on the energy reserves stored during the preceding phyllosoma phase, and hence the duration of the pueruli phase is constrained by these limited reserves (Jeffs et al., 1999; Fitzgibbon et al., 2014). Therefore, the ability of the pueruli to detect any cue from settlement habitats provides selective advantages (e.g., Gebauer et al., 2003).

6.3 Habitat change

Results from the two field experiments conducted for this project showed that recruitment of *Jasus edwardsii* is enhanced in kelp habitat. Catches of the pueruli and early benthic phase (EBP) on crevice collectors with giant kelp attached were higher than controls without giant kelp, suggesting that coverage of giant kelp on natural reefs should result in higher pueruli settlement. Overnight survival of tethered EBP was also higher in kelp habitat, suggesting that the structural complexity of this habitat, or differences in habitat-associated predators, may have contributed to reduced predation events. Climate change induced loss of the kelp habitat would thus be expected to affect settlement and subsequent recruitment of lobsters to this valuable fishery in the east coast of Tasmania (Figure 6.3).

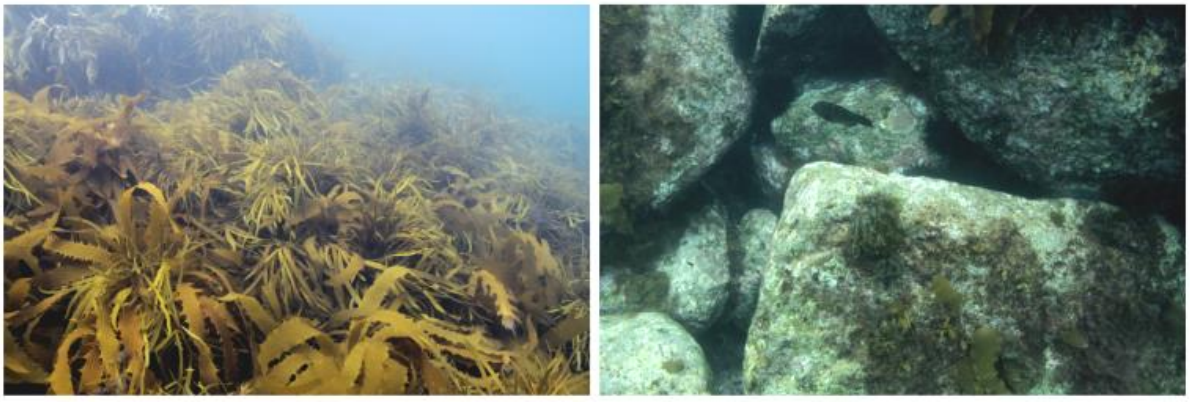


Figure 6.3. Habitat changes in shallow water coastal reefs on the east coast of Tasmania. In the left picture a natural kelp habitat composed by *Phyllospora comosa*, *Ecklonia radiata* and *Lessonia corrugata*. On the right, kelp cover has been lost through overgrazing by a species of urchin that has extended its range into Tasmania over the last three decades due to climate change.

Higher pueruli settlement on collectors with attached natural giant kelp than collectors with plastic kelp and controls without attachments, suggest that pueruli were receptive to chemical cues from the kelp, in addition to the physical structure. However, in subsequent laboratory experiments pueruli were not attracted to water with *M. pyrifera* exudates (Chapter 3), suggesting that other cues associated with natural kelp could explain the differences in pueruli abundance associated with this macroalgae. For example, we did not use the kelp

holdfast to generate the chemical cues in the laboratory which is known to provide a habitat for several spiny lobster species (e.g. Anderson et al., 2005). Also, the concentration of exudates from the kelp used in the laboratory experiment was likely to be higher than in the natural environment. Additional research is required to examine the mechanism of pueruli attraction to natural *M. pyrifera*.

Structured habitats, such as seagrass beds, mangroves, corals, mussels and kelp can provide the necessary resources and environmental conditions to facilitate the settlement and survival of many other species (Grutter and Irving, 2007; Halpern et al., 2007; Almanza et al., 2012). For example, it is well established that mangroves enhance the settlement of some fish species where the two most important pressures governing this habitat selection are the risk of predation and the availability of food (e.g. Laegdsgaard and Johnson, 2001). The EBP of *J. edwardsii* inhabit small holes and crevices scaled to their body size, and forage only at night across small areas presumably to reduce encounter rates with predators (Edmunds, 1995; Butler et al., 1999). We found that the overnight predation of tethered EBP was lower in the kelp habitat than in the urchin barren indicating that this habitat reduces predation encounters, possibly by obstructing prey detection and also by changing the ability of predators to manoeuvre and capture prey (e.g. Syms and Jones, 2000; Rogers et al., 2014). The presence of kelp is also likely to increase the availability of food for juvenile lobsters (Caputi et al., 2013) and modify the predator composition and abundance (Pérez-Matus and Shima, 2010), although these factors were not directly examined in this present study.

These results of these field experiments suggest that kelp habitat "facilitates" (sensu Bruno et al., 2003) the recruitment process for *J. edwardsii,* but it is possible that this species is less vulnerable to a loss of kelp habitat than some other lobster species (Wahle and Steneck, 1992; Butler et al., 2006). Change in kelp abundance would not be expected to create localised extinction of lobsters, but rather reduce productivity due to a reduction in recruitment. Field

studies show that lobsters inhabit urchin barrens and probably may successfully recruit on them, although abundance of sub-adults *J. edwardsii* is generally low in this habitat (Johnson et al., 2013). Settlement trends on collectors have been related to the future exploitable biomass (Gardner et al., 2001; Booth and McKenzie, 2009; Linnane et al., 2014). The inclusion of these regional settlement trends into management decisions need to be cautiously considered because potential post-settlement mortality processes can occur. Kelp depletion due to climate change in combination with fishery effects (e.g. Johnson et al., 2011) could create a mismatch in the relationship between settlement in artificial collectors and future fishable biomass in the east coast of Tasmania.

6.4 Conclusion

The research presented in this thesis revealed results and patterns that can be considered to develop new testable hypotheses. Large scale environment variables influence the synchronism in settlement at a regional scale in Australia and New Zealand, probably controlling the abundance and spatial distribution of the competent phyllosoma larvae. Pueruli can detect chemical cues from coastal waters and sound from a reef, which might assist the orientation to coastal and settlement habitats. However, the distance at which these cues may be used by pueruli needs more empirical research. Kelp habitats enhance the settlement and provide protection to early benthic juveniles during nocturnal activity. A quantification of the effect of this habitat change could be possible comparing between undersize lobsters in commercial catches (or other source of fishery recruitment) and pueruli monitoring in crevice collectors along the east coast of Tasmania. If habitat change is reducing survival a mismatch of the relationship between puerulus in collectors and fishery recruitment is expected, with fewer undersize lobsters for a given level of puerulus settlement.

Overall, the evolutionary strategy in this lobster species is one of high annual fecundity and an active searching process during settlement to compensate potential higher mortality during long larval development and dispersal (Cobb et al., 1997; Booth, 2001). Large scale climate/oceanic processes that are positive for settlement in one region in some years can have the opposite effect in other areas showing higher annual settlement variability in a particular site. Lobsters are long-live invertebrates where a local population might resist some years of lower recruitment. This implies also some resilience of the fishery across a very broad scale (southern Australia and New Zealand), and also some plasticity in the population to adjust to environmental changes associated with future climate changes. However, local habitat alterations may have some important effects in the future recruitment of this valuable fishery resource.

REFERENCES

Almanza, V., Buschmann, A. H., Hernandez-Gonzalez, M. C., and Henriquez, L. A. 2012. Can giant kelp (*Macrocystis pyrifera*) forests enhance invertebrate recruitment in southern Chile? Marine Biology Research, 8: 855-864.

Anderson, M. J., Diebel, C. E., Blom, W. M., and Landers, T. J. 2005. Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. Journal of Experimental Marine Biology and Ecology, 320: 35-56.

Ashok, K., Nakamura, H., and Yamagata, T. 2007. Impacts of ENSO and Indian Ocean dipole events on the Southern Hemisphere storm-track activity during austral winter. Journal of Climate, 20: 3147-3163.

Ashok, K., and Saji, N. H. 2007. On the impacts of ENSO and Indian Ocean dipole events on sub-regional Indian summer monsoon rainfall. Natural Hazards, 42: 273-285.

Atema, J., Brönmark, C., and Hansson, L. 2012. Aquatic odour dispersal fields: opportunities and limits of detection, communication, and navigation. *In* Chemical Ecology in Aquatic Systems, pp. 1-18. Ed. by C. Brönmark, and L. Hansson. Oxford University Press Oxford.

Au, W. W. L., and Hastings, M. C. 2009. Principles of marine bioacoustics, Springer, New York. 679 pp.

Bates, A. E., Barrett, N. S., Stuart-Smith, R. D., Holbrook, N. J., Thompson, P. A., and Edgar, G. J. 2014. Resilience and signatures of tropicalization in protected reef fish communities. Nature Climate Change, 4: 62-67.

Boland, F. M., and Church, J. A. 1981. The East Australian Current 1978. Deep-Sea Research Part a-Oceanographic Research Papers, 28: 937-957.

Booth, J. D., and Tarring, S. C. 1986. Settlement of the red rock lobster, *Jasus edwardsii*, near Gisborne, New Zealand. New Zealand Journal of Marine and Freshwater Research, 20: 291-297.

Booth, J. D. 1989. Occurrence of the puerulus stage of the rock lobster, *Jasus edwardsii* at the New Plymouth Power Station, New-Zealand. New Zealand Journal of Marine and Freshwater Research, 23: 43-50.

Booth, J. D., and Stewart, R. A. 1993. Puerulus settlement in the red rock lobster, *Jasus edwardsii*. New Zealand Fisheries Assesment Research Document, 93/5.

Booth, J. D. 1994. *Jasus edwardsii* larval recruitment off the east coast of New Zealand. Crustaceana, 66: 295-317.

Booth, J. D., and Phillips, B. F. 1994. Early life history of spiny lobster. Crustaceana, 66: 271-294.

Booth, J. D., Bradford, E., and Renwick, J. 2000. *Jasus edwardsii* puerulus settlement levels examined in relation to the ocean environment and to subsequent juvenile and recruitmen abundance. New Zealand Fisheries Assessment Report 2000/34: 48 p.

Booth, J. D., and Ovenden, J. R. 2000. Distribution of *Jasus* spp. (Decapoda: Palinuridae) phyllosomas in southern waters: implications for larval recruitment. Marine Ecology Progress Series, 200: 241–255.

Booth, J. D. 2001. Habitat preferences and behaviour of newly settled *Jasus edwardsii* (Palinuridae). Marine and Freshwater Research, 52: 1055-1065.

Booth, J. D. 2006. *Jasus* species. *In* Lobsters: biology, management, aquaculture and fisheries, pp. 340-358. Ed. by B. F. Phillips. Blackwell Publishing, Oxford.

Booth, J. D., and McKenzie, A. 2009. Strong relationships between levels of puerulus settlement and recruited stock abundance in the red rock lobster (*Jasus edwardsii*) in New Zealand. Fisheries Research, 95: 161-168.

Bradford, R. W., Bruce, B. D., Chiswell, S. M., Booth, J. D., Jeffs, A., and Wotherspoon, S. 2005. Vertical distribution and diurnal migration patterns of *Jasus edwardsii* phyllosomas off the east coast of the North Island, New Zealand. New Zealand Journal of Marine and Freshwater Research, 39: 593-604.

Bradford, R. W., Griffin, D., and Bruce, B. B. 2015. Estimating the duration of the pelagic phyllosoma phase of the southern rock lobster, *Jasus edwardsii* (Hutton). Marine and Freshwater Research, 66: 213–219.

Breithaupt, T., and Thiel, M. 2012. Chemical communication in crustaceans, Springer, London. 565 pp.

Briffa, M., de la Haye, K., and Munday, P. L. 2012. High CO 2 and marine animal behaviour: potential mechanisms and ecological consequences. Marine Pollution Bulletin, 64: 1519-1528.

Briones-Fourzan, P., Candela, J., and Lozano-Alvarez, E. 2008. Postlarval settlement of the spiny lobster *Panulirus argus* along the Caribbean coast of Mexico: Patterns, influence of physical factors, and possible sources of origin. Limnology and Oceanography, 53: 970-985.

Broitman, B. R., Blanchette, C. A., Menge, B. A., Lubchenco, J., Krenz, C., Foley, M., Raimondi, P. T., et al. 2008. Spatial and temporal patterns of invertebrate recruitment along the West Coast of the United States. Ecological Monographs, 78: 403-421.

Bruce, B., Bradford, R., Griffin, D., Gardner, C., and Young, J. 2000. A synthesis of existing data on larval rock lobster distribution in southern Australia. Final Report to the Fisheries Research and Development Corporation, Proyect 96/107, CSIRO Marine and Atmospheric Research: 57 p.

Bruce, B. D., Bradford, R., Griffin, D., Gardner, C., and Young, J. 2007. Larval transport and recruitment processes of southern rock lobster. Fisheries Research and Development Corporation, Project 2002/007: CSIRO Marine and Atmospheric Research, Hobart.

Bruno, J. F., Stachowicz, J. J., and Bertness, M. D. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution, 18: 119-125.

Butler, M. J., MacDiarmid, A. B., and Booth, J. D. 1999. The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. Marine Ecology Progress Series, 188: 179-191.

Butler, M. J., Steneck, R. S., and Herrnkind, W. F. 2006. Juvenile and adult ecology. *In* Lobsters: Biology, Management, Aquaculture and Fisheries, pp. 263-309. Ed. by B. F. Phillips. Blackwell Scientific Press, Oxford.

Byrnes, J. E., Reed, D. C., Cardinale, B. J., Cavanaugh, K. C., Holbrook, S. J., and Schmitt, R. J. 2011. Climate-driven increases in storm frequency simplify kelp forest food webs. Global Change Biology, 17: 2513-2524.

Cai, W., Van Rensch, P., and Cowan, T. 2011. Influence of global-scale variability on the subtropical ridge over southeast Australia. Journal of Climate, 24: 6035-6053.

Caputi, N. 2008. Impact of the Leeuwin Current on the spatial distribution of the puerulus settlement of the western rock lobster (*Panulirus cygnus*) and implications for the fishery of Western Australia. Fisheries Oceanography, 17: 147-152.

Caputi, N., Lestang, S., Frusher, S., and Wahle, R. A. 2013. The impact of climate change on exploited lobster stocks. *In* Lobsters: Biology, Management, Aquaculture and Fisheries, Second Edition, pp. 84-112. Ed. by B. F. Phillips. Wiley Online Library.

Castillo-Jordan, C. A., Klaer, N. L., Tuck, G. N., Frusher, S. D., Cubillos, L. A., Tracey, S. R., and Salinger, M. J. 2015. Coincident recruitment patterns of Southern Hemisphere fishes. Canadian Journal of Fisheries and Aquatic Sciences, 72: 1-9.

Cato, D. H., and McCauley, R. 2002. Australian research in ambient sea noise. Acoustics Australia, 30: 1-13.

Chiswell, S. M., and Booth, J. D. 1999. Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. Marine Ecology Progress Series, 183: 227-240.

Chiswell, S. M., Wilkin, J., Booth, J. D., and Stanton, B. 2003. Trans-Tasman Sea larval transport: Is Australia a source for New Zealand rock lobsters? Marine Ecology Progress Series, 247: 173-182.

Cobb, J. S., Booth, J. D., and Clancy, M. 1997. Recruitment strategies in lobsters and crabs: a comparison. Marine and Freshwater Research, 48: 797-806.

Cohen, J. 1988. Statistical power analysis for the behavioral science, Lawrence Erlbaum, New York, New York, USA.

Cohen, P. J., and Gardner, C. 2007. Regional patterns in puerulus catches from eastern and western Tasmania. Journal of Crustacean Biology, 27: 592-596.

Colton, A. R., Wilberg, M. J., Coles, V. J., and Miller, T. J. 2014. An evaluation of the synchronization in the dynamics of blue crab (*Callinectes sapidus*) populations in the western Atlantic. Fisheries Oceanography, 23: 132-146.

Cowen, R. K., Paris, C. B., and Srinivasan, A. 2006. Scaling of connectivity in marine populations. Science, 311: 522-527.

Cowen, R. K., Gawarkiewic, G., Pineda, J., Thorrold, S. R., and Werner, F. E. 2007. Population connectivity in marine systems: an overview. Oceanography, 20: 14-21.

Cowen, R. K., and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. Annual review of marine science, 1: 443-466.

Cox, S. L., and Bruce, M. P. 2003. Feeding behaviour and associated sensory mechanisms of stage I-III phyllosoma of *Jasus edwardsii* and *Jasus verreauxi*. Journal of the Marine Biological Association of the United Kingdom, 83: 465-468.

Crawley, M. J. 2013. The R book, Wiley, Chichester, England ; Hoboken, N.J. xxiv, 1051 pp.

Cresswell, G. 2000. Currents of the continental shelf and upper slope of Tasmania Papers and Proceedings of the Royal Society of Tasmania, 133: 21-30.

Darwin, C. 1913. A naturalist's voyage round the world - the voyage of the Beagle, John Murray, London. 538 pp.

Dayton, P. K. 2003. The importance of the natural sciences to conservation. The American Naturalist, 162: 1-13.

de Lestang, S., Caputi, N., Feng, M., Denham, A., Penn, J., Slawinski, D., Pearce, A., et al. 2015. What caused seven consecutive years of low puerulus settlement in the western rock lobster fishery of Western Australia? ICES Journal of Marine Science, 72(S1): i49-i58.

Edmunds, M. 1995. The ecology of the juvenile southern rock lobster, *Jasus edwardsii* (Hutton 1875) (Palinuridae). University of Tasmania, Hobart, Australia.

Ehrhardt, N. M., and Fitchett, M. D. 2010. Dependence of recruitment on parent stock of the spiny lobster, Panulirus argus, in Florida. Fisheries Oceanography, 19: 434-447.

Erzini, K. 2005. Trends in NE Atlantic landings (southern Portugal): identifying the relative importance of fisheries and environmental variables. Fisheries Oceanography, 14: 195-209.

Fiksen, O., Jorgensen, C., Kristiansen, T., Vikebo, F., and Huse, G. 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Marine Ecology Progress Series, 347: 195-205.

Filbee-Dexter, K., and Scheibling, R. E. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Marine Ecology Progress Series, 495: 1-25.

Fitzgibbon, Q. P., Battaglene, S. C., and Jeffs, A. G. 2014. The achilles heel for spiny lobsters: the energetic of the non-feeding post-larval stage. Fish and Fisheries, 15: 312-326.

Flukes, E. B., Johnson, C. R., and Ling, S. D. 2012. Forming sea urchin barrens from the inside out: an alternative pattern of overgrazing. Marine Ecology Progress Series, 464: 179-194.

Forward, R. B., Tankersley, R. A., Smith, K. A., and Welch, J. M. 2003. Effect of chemical cues on orientation of blue crab, *Callinectes sapidus* megalopae in flow: implications for location of nursery areas. Marine Biology, 142: 747-756.

Frusher, S., Prescott, J., and Edmunds, M. 1999. Southern rock lobsters. *In* Under Southern Seas. The Ecology of Australia's Rocky Reefs, pp. 106-113. Ed. by N. Andrew. University of New South Wales Press, Sydney.

Gardner, C., Frusher, S. D., Kennedy, R. B., and Cawthorn, A. 2001. Relationship between settlement of southern rock lobster pueruli, *Jasus edwardsii*, and recruitment to the fishery in Tasmania, Australia. Marine and Freshwater Research, 52: 1271-1275.

Gebauer, P., Paschke, K., and Anger, K. 2002. Metamorphosis in a semiterrestrial crab, *Sesarma curacaoense*: intra- and interspecific settlement cues from adult odors. Journal of Experimental Marine Biology and Ecology, 268: 1-12.

Gebauer, P., Paschke, K., and Anger, K. 2003. Delayed metamorphosis in Decapod crustaceans: evidence and consequences. Revista Chilena de Historia Natural, 76: 169-175.

Gerlach, G., and Artema, J. 2012. The use of chemical cues in habitat recognition and settlement. Chemical Ecology in Aquatic Systems: 72-89.

Goldstein, J. S., and Butler, M. J. 2009. Behavioral enhancement of onshore transport by postlarval Caribbean spiny lobster (*Panulirus argus*). Limnology and Oceanography, 54: 1669-1678.

Gordon, N. D. 1985. The southern oscillation: a New Zealand perspective. Journal of the Royal Society of New Zealand, 15: 137-155.

Green, B. S., Gardner, C., and Kennedy, R. B. 2009. Generalised linear modelling of fecundity at length in southern rock lobsters, *Jasus edwardsii*. Marine Biology, 156: 1941-1947.

Grutter, A., and Irving, A. D. 2007. Positive interactions in marine communities. *In* Marine Ecology, pp. 110-137. Ed. by S. D. Connell, and B. M. Gillanders. Oxford University Press.

Halpern, B. S., Silliman, B. R., Olden, J. D., Bruno, J. P., and Bertness, M. D. 2007. Incorporating positive interactions in aquatic restoration and conservation. Frontiers in Ecology and the Environment, 5: 153-160.

Harley, C. D. G., Anderson, K. M., Demes, K. W., Jorve, J. P., Kordas, R. L., Coyle, T. A., and Graham, M. H. 2012. Effects of climate change on global seaweed communities. Journal of Phycology, 48: 1064-1078.

Harrell, F. E. 2015. rms: Regression Modeling Strategies. R package version 4.3-0. https://cran.r-project.org/web/packages/rms/index.html. Accessed May 2015.

Harrington, D. P., and Fleming, T. R. 1982. A class of rank test procedures for censored survival-data. Biometrika, 69: 553-566.

Hartmann, K., Gardner, C., and Hobday, D. 2013. Tasmanian rock lobster fishery 2011/12. Fishery Assessment Report, The Institute for Marine and Antarctic Studies: 61.

Hayakawa, Y., Booth, J. D., Nishida, S., Sekiguchi, H., Saisho, T., and Kittaka, J. 1990. Daily settlement of the puerulus stage of the red rock lobster *Jasus edwardsii* at Castlepoint, New Zealand. Nippon Suisan Gakkaishi, 56: 1703-1716.

Hayakawa, Y., and Nishida, S. 2002. Diel behavior of the puerulus and the first instar juvenile of the red rock lobster, *Jasus edwardsii*. Fisheries Science, 68: 393-396.

Hinojosa, I. A., Green, B., Gardner, C., and Jeffs, A. 2015. Settlement and early survival of southern rock lobster, *Jasus edwardsii*, under climate-driven decline of kelp habitats. ICES Journal of Marine Science, 72(S1): i59-i68.

Hobday, A. J., and Pecl, G. T. 2014. Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Reviews in Fish Biology and Fisheries, 24: 415-425.

Holmes, E. E., Ward, E. J., and Wills, K. 2012. MARSS: Multivariate autoregressive state-space models for analyzing time-series data. R Journal, 4: 11-19.

Horner, A. J., Nickles, S. P., Weissburg, M. J., and Derby, C. D. 2006. Source and specificity of chemical cues mediating shelter preference of Caribbean spiny lobsters (*Panulirus argus*). Biological Bulletin, 211: 128-139.

Hothorn, T., Zeileis, A., Farebrother, R. W., Cummins, C., Millo, G., and Mitchell, D. 2013. lmtest: testing linear regression models. http://cran.r-project.org/web/packages/lmtest. Accessed May 2015.

Huijbers, C. M., Nagelkerken, I., Lossbroek, P. A. C., Schulten, I. E., Siegenthaler, A., Holderied, M. W., and Simpson, S. D. 2012. A test of the senses: Fish select novel habitats by responding to multiple cues. Ecology, 93: 46-55.

Hyndman, R. J., and Athanasopoulos, G. 2014. Forecasting: Principles and Practice. http://www.otexts.org/fpp. Accessed May 2015.

Igulu, M. M., Nagelkerken, I., Van Der Beek, M., Schippers, M., Van Eck, R., and Mgaya, Y. D. 2013. Orientation from open water to settlement habitats by coral reef fish: Behavioral flexibility in the use of multiple reliable cues. Marine Ecology Progress Series, 493: 243-257.

Jackson, G. A. 1986. Interaction of physical and biological processes in the settlement of planktonic larvae. Bulletin of Marine Science, 39: 202-212.

Jeffs, A. G., Diebel, C. E., and Hooker, S. H. 1997. Arrangement and significance of pinnate sensory setae on antennae of the puerulus and post-puerulus of the spiny lobster, *Jasus edwardsii* (Palinuridae). Marine and Freshwater Research, 48: 681-686.

Jeffs, A. G., Willmott, M. E., and Wells, R. M. G. 1999. The use of energy stores in the puerulus of the spiny lobster *Jasus edwardsii* across the continental shelf of New Zealand. Comparative Biochemistry and Physiology, 123A: 351-357.

Jeffs, A. G., and Holland, R. C. 2000. Swimming behaviour of the puerulus of the spiny lobster *Jasus edwardsii* (Hutton,1875). Crustaceana, 73: 847–856.

Jeffs, A. G., Chiswell, S. M., and Booth, J. D. 2001a. Distribution and condition of pueruli of the spiny lobster *Jasus edwardsii* offshore from north-east New Zealand. Marine and Freshwater Research, 52: 1211-1216.

Jeffs, A. G., Nichols, P. D., and Bruce, M. P. 2001b. Lipid reserves used by pueruli of the spiny lobster *Jasus edwardsii* in crossing the continental shelf of New Zealand. Comparative Biochemistry and Physiology, 129A: 305-311.

Jeffs, A. G., Tolimieri, N., and Montgomery, J. C. 2003. Crabs on cue for the coast: the use of underwater sound for orientation by pelagic crab stages. Marine and Freshwater Research 54: 841-845.

Jeffs, A. G., Montgomery, J. C., and Tindle, C. T. 2005. How do spiny lobster post-larvae find the coast? New Zealand Journal of Marine and Freshwater Research, 39: 605-617.

Jeffs, A. G., Gardner, C., and Cockcroft, A. 2013. *Jasus* and *Sagmariasus* species. *In* Lobsters: Biology, Management, Aquaculture and Fisheries, Second Edition edn, pp. 259-288. Ed. by B. F. Phillips. Wiley & Sons, Ltd.

Jiang, N., Griffiths, G., and Lorrey, A. 2013. Influence of large-scale climate modes on daily synoptic weather types over New Zealand. International Journal of Climatology, 33: 499-519.

Johnson, C. R., Banks, S. C., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J., Frusher, S. D., et al. 2011. Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. Journal of Experimental Marine Biology and Ecology, 400: 17-32.

Johnson, C. R., Ling, S. D., Sanderson, C., Dominguez, J. G. S., Flukes, E. B., Frusher, S. D., Gardner, C., et al. 2013. Rebuilding ecosystem resilience: Assessment of management options to minimise formation of 'barrens' habitat by the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania. Final Report to the Fisheries Research & Development Corporation, Project Number 2007/045: 356.

Katara, I., Pierce, G. J., Illian, J., and Scott, B. E. 2011. Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. Hydrobiologia, 670: 49-65.

Kellogg, W. N. 1953. Bibliography of the noises made by marine organisms. The American Museum of Natural History, 1611: 1-5.

Keough, M. J. 1983. Patterns of recruitment of ressile invertebrates in two subtidal habitats. Journal of Experimental Marine Biology and Ecology, 66: 213-245.

Keough, M. J., and Swearer, S. E. 2007. Early life histories of marine invertebrates and fishes. *In* Marine Ecology, pp. 19-46. Ed. by S. D. Connell, and B. M. Gillanders. Oxford University Press, Oxford.

Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G., and Pineda, J. 2002. Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science, 70: 309-340.

Knudsen, V. O., Alford, R. S., and Emling, J. W. 1948. Underwater Ambient Noise. Journal of Marine Research, 7: 410-429.

Kough, A. S., Paris, C. B., and Butler, M. J. 2013. Larval connectivity and the international management of fisheries. PLoS ONE, 8: e64970.

Kough, A. S., Paris, C. B., and Staaterman, E. 2014. In situ swimming and orientation behavior of spiny lobster (*Panulirus argus*) postlarvae. Marine Ecology Progress Series, 504: 207-219.

Kovalenko, K. E., Thomaz, S. M., and Warfe, D. M. 2012. Habitat complexity: approaches and future directions. Hydrobiologia, 685: 1-17.

Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S., and Liu, W. C. 2001. Pseudoreplication in playback experiments, revisited a decade later. Animal Behaviour, 61: 1029-1033.

Laegdsgaard, P., and Johnson, C. 2001. Why do juvenile fish utilise mangrove habitats? Journal of Experimental Marine Biology and Ecology, 257: 229-253.

Lecchini, D., Miura, T., Lecellier, G., Banaigs, B., and Nakamura, Y. 2014. Transmission distance of chemical cues from coral habitats: implications for marine larval settlement in context of reef degradation. Marine Biology, 161: 1677-1686.

Leis, J. M., Carson-Ewart, B. M., and Cato, D. H. 2002. Sound detection *in situ* by the larvae of a coral-reef damselfish (Pomacentridae). Marine Ecology Progress Series, 232: 259-268.

Lesser, J. H. R. 1978. Phyllosoma larvae of *Jasus edwardsii* (Hutton) (Crustacea, Decapoda, Palinuridae) and their distribution off the East Coast of the North Island, New Zealand. New Zealand Journal of Marine and Freshwater Research, 12: 357-370.

Levin, L. A. 2006. Recent progress in understanding larval dispersal: new directions and digressions. Integrative and Comparative Biology, 46: 282-297.

Liebhold, A., Koenig, W. D., and Bjornstad, O. N. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology Evolution and Systematics, 35: 467-490.

Ling, S. D. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia, 156: 883-894.

Ling, S. D., Johnson, C. R., Frusher, S. D., and Ridgway, K. R. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences of the United States of America, 106: 22341-22345.

Linnane, A., Gardner, C., Hobday, D., Punt, A., McGarvey, R., Feenstra, J., Matthews, J., et al. 2010a. Evidence of large-scale spatial declines in recruitment patterns of southern rock lobster *Jasus edwardsii*, across south-eastern Australia. Fisheries Research, 105: 163-171.

Linnane, A., James, C., Middleton, J., Hawthorne, P., and Hoare, M. 2010b. Impact of wind stress anomalies on the seasonal pattern of southern rock lobster (*Jasus edwardsii*) settlement in South Australia. Fisheries Oceanography, 19: 290-300.

Linnane, A., McGarvey, R., Gardner, C., Walker, T. I., Matthews, J., Green, B., and Punt, A. E. 2014. Large-scale patterns in puerulus settlement and links to fishery recruitment in the southern rock lobster (*Jasus edwardsii*), across south-eastern Australia. ICES Journal of Marine Science, 71: 528-536.

Little, R. J. A. 1988. Missing-data adjustments in large surveys. Journal of Business & Economic Statistics, 6: 287-296.

Lumley, T. 2013. leaps: regression subset selection package. http://cran.r-project.org/web/packages/leaps. Accessed May 2015.

Macmillan, D. L., Phillips, B. F., and Coyne, J. A. 1992. Further observations on the antennal receptors of rock lobsters and their possible involvement in puerulus stage navigation. Marine Behaviour and Physiology, 19: 211-225.

Manderson, J. P. 2008. The spatial scale of phase synchrony in winter flounder (*Pseudopleuronectes americanus*) production increased among southern New England nurseries in the 1990s. Canadian Journal of Fisheries and Aquatic Sciences, 65: 340-351.

Mann, D. A., Casper, B. M., Boyle, K. S., and Tricas, T. C. 2007. On the attraction of larval fishes to reef sounds. Marine Ecology Progress Series, 338: 307-310.

Manriquez, P. H., and Castilla, J. C. 2011. Behavioural traits of competent *Concholepas concholepas* (loco) larvae. Marine Ecology Progress Series, 430: 207-221.

Marshall, G. J. 2003. Trends in the southern annular mode from observations and reanalyses. Journal of Climate, 16: 4134-4143.

Mazzuco, A., Christofoletti, R., Pineda, J., Starczak, V., and Ciotti, A. 2015. Temporal variation in intertidal community recruitment and its relationships to physical forcings, chlorophyll-a concentration and sea surface temperature. Marine Biology, 162: 1705-1725.

McWilliam, P. S., and Phillips, B. F. 1997. Metamorphosis of the final phyllosoma and secondary lecithotrophy in the puerulus of *Panulirus cygnus* George: a review. Marine and Freshwater Research, 48: 783-790.

Meinfelder, F. 2011. BaBooN: Bayesian bootstrap predictive mean matching – multiple and single imputation for discrete data. http://cran.r-project.org/package=BaBooN. Accessed May 2015.

Meyers, G., McIntosh, P., Pigot, L., and Pook, M. 2007. The years of El Niño, La Niña, and interactions with the tropical Indian Ocean. Journal of Climate, 20: 2872-2880.

Miller, A. 2002. Subset selection in regression, Chapman & Hall/CRC Press, Boca Raton, Florida. 256 pp.

Mills, D. J., Gardner, C., and Oliver, M. 2005. Survival and movement of naive juvenile spiny lobsters returned to the wild. Journal of Experimental Marine Biology and Ecology, 324: 20-30.

Mills, D. J., Gardner, C., and Johnson, C. R. 2006. Experimental reseeding of juvenile spiny lobsters (*Jasus edwardsii*): Comparing survival and movement of wild and naive lobsters at multiple sites. Aquaculture, 254: 256-268.

Mills, D. J., Johnson, C. R., and Gardner, C. 2008. Bias in lobster tethering experiments conducted for selecting low-predation release sites. Marine Ecology Progress Series, 364: 1-13.

Mislan, K. A. S., and Babcock, R. C. 2008. Survival and behaviour of juvenile red rock lobster, *Jasus edwardsii*, on rocky reefs with varying predation pressure and habitat complexity. Marine and Freshwater Research, 59: 246-253.

Montgomery, J. C., Jeffs, A., Simpson, S. D., Meekan, M., and Tindle, C. 2006. Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. Advances in Marine Biology, 51: 143-196.

Nedelec, S. L., Simpson, S. D., Holderied, M., Radford, A. N., Lecellier, G., Radford, C., and Lecchini, D. 2015. Soundscapes and living communities in coral reefs: temporal and spatial variation. Marine Ecology Progress Series, 524: 125-135.

Nilsson, G. E., Dixson, D. L., Domenici, P., McCormick, M. I., Sørensen, C., Watson, S.-A., and Munday, P. L. 2012. Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. Nature Climate Change, 2: 201-204.

Oke, P. R., Sakov, P., Cahill, M. L., Dunn, J. R., Fiedler, R., Griffin, D. A., Mansbridge, J. V., et al. 2013. Towards a dynamically balanced eddy-resolving ocean reanalysis: BRAN3. Ocean Modelling, 67: 52-70.

Oliver, E. C. J., and Holbrook, N. J. 2014. Extending our understanding of South Pacific gyre "spin-up": Modeling the East Australian Current in a future climate. Journal of Geophysical Research-Oceans, 119: 2788-2805.

Paradis, E., Baillie, S. R., Sutherland, W. J., and Gregory, R. D. 2000. Spatial synchrony in populations of birds: Effects of habitat, population trend, and spatial scale. Ecology, 81: 2112-2125.

Paris, C. B., Atema, J., Irisson, J.-O., Kingsford, M., Gerlach, G., and Guigand, C. M. 2013. Reef odor: a wake up call for navigation in reef fish larvae. PLoS ONE, 8: e72808.

Paul, V. J., Ritson-Williams, R., and Sharp, K. 2011. Marine chemical ecology in benthic environments. Natural Product Reports, 28: 345-387.

Pérez-Matus, A., and Shima, J. S. 2010. Disentangling the effects of macroalgae on the abundance of temperate reef fishes. Journal of Experimental Marine Biology and Ecology, 388: 1-10.

Phillips, B. F., Rimmer, D. W., and Reid, D. D. 1978. Ecological investigations of the late-stage phyllosoma and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. Marine Biology, 45: 347–357.

Phillips, B. F., and Macmillan, D. L. 1987. Antennal receptors in peurulus and postpuerulus stages of the rock lobster *Panulirus cygnus* (Decapoda, Palinuridae) and their potential role in puerulus navigation. Journal of Crustacean Biology, 7: 122-135.

Phillips, B. F., Melville-Smith, R., Cheng, Y. W., and Rossbach, M. 2001. Testing collector designs for commercial harvesting of western rock lobster (*Panilirus cygnus*) puerulus. Marine and Freshwater Research, 52: 1465-1473.

Phillips, B. F., Cheng, Y. W., Cox, C., Hunt, J., Jue, N. K., and Melville-Smith, R. 2005. Comparison of catches on two types of collector of recently settled stages of the spiny lobster (*Panulirus argus*), Florida, United States. New Zealand Journal of Marine and Freshwater Research, 39: 715-722.

Phillips, B. F., Booth, J. D., Cobb, J. S., Jeffs, A. G., and McWilliam, P. 2006. Larval and postlarval ecology. *In* Lobsters: Biology, Management, Aquaculture and Fisheries, pp. 231-262. Ed. by B. F. Phillips. Blackwell Publishing Ltd.

Phillips, B. F., and McWilliam, P. S. 2009. Spiny lobster development: where does successful metamorphosis to the puerulus occur?: A review. Reviews in Fish Biology and Fisheries, 19: 193-215.

Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a Southern California rocky shore. Marine Ecology Progress Series, 107: 125-138.

Pineda, J., Hare, J. A., and Sponaugle, S. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography, 20: 22-39.

Pineda, J., Porri, F., Starczak, V., and Blythe, J. 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. Journal of Experimental Marine Biology and Ecology, 392: 9-21.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R-Core-Team. 2015. nlme: Linear and nonlinear mixed effects models. http://cran.r-project.org/package=nlme. Accessed May 2015

Poulin, E., Palma, A. T., Leiva, G., Narvaez, D., Pacheco, R., Navarrete, S. A., and Castilla, J. C. 2002. Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in Central Chile. Limnology and Oceanography, 47: 1248-1255.

Quinn, G. P., and Keough, M. J. 2002. Experimental design and data analysis for biologists, Cambridge University Press, Cambridge. 537 pp.

R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radford, C. A., Jeffs, A. G., and Montgomery, J. C. 2007. Directional swimming behavior by five species of crab postlarvae in response to reef sound. Bulletin of Marine Science, 80: 369-378.

Radford, C. A., Jeffs, A. G., and Montgomery, J. C. 2008a. Orientated swimming behaviour of crab postlarvae in response to reef sound. Bioacoustics, 17: 87-89.

Radford, C. A., Jeffs, A. G., Tindle, C., and Montgomery, J. C. 2008b. Resonating sea urchin skeletons create coastal choruses. Marine Ecology Progress Series, 362: 37-43.

Radford, C. A., Jeffs, A. G., Tindle, C. T., and Montgomery, J. C. 2008c. Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. Oecologia, 156: 921-929.

Radford, C. A., Stanley, J. A., Tindle, C. T., Montgomery, J. C., and Jeffs, A. G. 2010. Localised coastal habitats have distinct underwater sound signatures. Marine Ecology Progress Series, 401: 21-29.

Radford, C. A., Stanley, J. A., Simpson, S. D., and Jeffs, A. G. 2011a. Juvenile coral reef fish use sound to locate habitats. Coral Reefs, 30: 295-305.

Radford, C. A., Tindle, C. T., Montgomery, J. C., and Jeffs, A. G. 2011b. Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. Marine Ecology Progress Series, 438: 167-174.

Radford, C. A., Stanley, J. A., and Jeffs, A. G. 2014. Adjacent coral reef habitats produce different underwater sound signatures. Marine Ecology Progress Series, 505: 19-28.

Renwick, J., and Thompson, D. 2006. The southern annular mode and New Zealand climate. Water & Atmosphere, 14: 24-25.

Ridgway, K. R., and Dunn, J. R. 2003. Mesoscale structure of the mean East Australian Current System and its relationship with topography. Progress in Oceanography, 56: 189-222.

Ridgway, K. R., and Condie, S. A. 2004. The 5500-km-long boundary flow off western and southern Australia. Journal of Geophysical Research-Oceans, 109: 1-18.

Ridgway, K. R. 2007. Long-term trend and decadal variability of the southward penetration of the East Australian Current. Geophysical Research Letters, 34.

Rogers, A., Blanchard, J. L., and Mumby, P. J. 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. Current Biology, 24: 1000-1005.

Saji, N. H., Goswami, B. N., Vinayachandran, P. N., and Yamagata, T. 1999. A dipole mode in the tropical Indian Ocean. Nature, 401: 360-363.

Sanderson, J. C. 1987. A survey of the *Macrocystis pyrifera* (L.) C. Agardh stocks on the east coast of Tasmania.Technical Report 21. Department of Sea Fisheries, Tasmania, Hobart, Tasmania. http://eprints.utas.edu.au/11925/.

Schott, F. A., Xie, S. P., and McCreary, J. P. 2009. Indian Ocean circulation and climate variability. Reviews of Geophysics, 47: 1-46.

Shanks, A. L. 2009. Pelagic larval duration and dispersal distance revisited. Biological Bulletin, 216: 373-385.

Shears, N. T., Babcock, R. C., and Salomon, A. K. 2008. Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. Ecol Appl, 18: 1860-1873.

Sheaves, M., Baker, R., Nagelkerken, I., and Connolly, R. M. 2014. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuaries and Coasts, 38: 401-414.

Simpson, S. D., Meekan, M., Montgomery, J., McCauley, R., and Jeffs, A. 2005. Homeward sound. Science, 308: 221-221.

Simpson, S. D., Meekan, M. G., Jeffs, A., Montgomery, J. C., and McCauley, R. D. 2008. Settlement-stage coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef noise. Animal Behaviour, 75: 1861-1868.

Staaterman, E., Paris, C. B., and Helgers, J. 2012. Orientation behavior in fish larvae: A missing piece to Hjort's critical period hypothesis. Journal of Theoretical Biology, 304: 188-196.

Staaterman, E., and Paris, C. B. 2014. Modelling larval fish navigation: the way forward. ICES Journal of Marine Science, 71: 918-924.

Stanley, J. A., Radford, C. A., and Jeffs, A. G. 2010. Induction of settlement in crab megalopae by ambient underwater reef sound. Behavioral Ecology, 21: 113-120.

Stanley, J. A., Radford, C. A., and Jeffs, A. G. 2011. Behavioural response thresholds in New Zealand crab megalopae to ambient underwater sound. PLoS ONE, 6: e28572.

Stanley, J. A., Radford, C. A., and Jeffs, A. G. 2012. Location, location, location: finding a suitable home among the noise. Proceedings of the Royal Society B-Biological Sciences, 279: 3622-3631.

Stanley, J. A., Hesse, J., Hinojosa, I. A., and Jeffs, A. G. 2015. Inducers of settlement and moulting in post-larval spiny lobster. Oecologia 178: 685-697.

Syms, C., and Jones, G. P. 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology, 81: 2714-2729.

Tapia-Lewin, S., and Pardo, L. M. 2014. Field assessment of the predation risk - food availability trade-off in crab megalopae settlement. PLoS ONE, 9: e95335.

Therneau, T. 2015. A package for survival snalysis in S. *In* version 2.38. http://CRAN.R-project.org/package=survival.

Tilburg, C. E., Hurlburt, H. E., O'Brien, J. J., and Shriver, J. F. 2001. The dynamics of the East Australian Current system: The Tasman Front, the East Auckland Current, and the East Cape Current. Journal of Physical Oceanography, 31: 2917-2943.

Underwood, A. J., and Fairweather, P. G. 1989. Supply-side ecology and benthic marine assemblages. Trends in Ecology & Evolution, 4: 16-20.

Verges, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., et al. 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proceedings of the Royal Society B-Biological Sciences, 281: 20140846.

Vermeij, M. J. A., Marhaver, K. L., Huijbers, C. M., Nagelkerken, I., and Simpson, S. D. 2010. Coral larvae move toward reef sounds. PLoS ONE, 5: e10660.

Villegas, M. J., Laudien, J., Sielfeld, W., and Arntz, W. E. 2008. *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales; Phaeophyceae) kelp habitat structures and associated macrobenthic community off northern Chile. Helgoland Marine Research, 62: S33-S43.

Wahle, R. A., and Steneck, R. S. 1991. Recruitment habitats and nursery grounds of the american lobster *Homarus americanus* - a demographic bottleneck. Marine Ecology Progress Series, 69: 231-243.

Wahle, R. A., and Steneck, R. S. 1992. Habitat restrictions in early benthic life - experiments on habitat selection and insitu predation with the american lobster. Journal of Experimental Marine Biology and Ecology, 157: 91-114.

Weiss, H. M., Lozano-Alvarez, E., Briones-Fourzan, P., and Negrete-Soto, F. 2006. Using red light with fixed-site video cameras to study the behavior of the spiny lobster, *Panulirus argus*, and associated animals at night and inside their shelters. Marine Technology Society Journal, 40: 86-95.

Weiss, H. M., Lozano-Alvarez, E., and Briones-Fourzan, P. 2008. Circadian shelter occupancy patterns and predator-prey interactions of juvenile Caribbean spiny lobsters in a reef lagoon. Marine Biology, 153: 953-963.

Wilkin, J. L., and Jeffs, A. G. 2011. Energetics of swimming to shore in the puerulus stage of a spiny lobster: Can a postlarval lobster afford the cost of crossing the continental shelf? Limnology and Oceanography: Fluids and Environments, 1: 163–175.

Zar, J. H. 2010. Biostatistical analysis, Prentice-Hall/Pearson, Upper Saddle River, N.J. xiii, 944 pp.

Zuur, A. F., Tuck, I. D., and Bailey, N. 2003. Dynamic factor analysis to estimate common trends in fisheries time series. Canadian Journal of Fisheries and Aquatic Sciences, 60: 542-552.

Zuur, A. F., and Pierce, G. J. 2004. Common trends in northeast Atlantic squid time series. Journal of Sea Research, 52: 57-72.

Publication list

7.1 Publication list from this thesis and related co-authorship

Hinojosa IA, Gardner C, Green BS, Jeffs A, Leon R & Linnane A. *In prep*. Broad scale patterns and environmental drivers of settlement in the southern rock lobster, *Jasus edwardsii. Fisheries Oceanography.*

Hinojosa IA, Gardner C, Green B, & Jeffs A. *In prep*. Coastal chemical cues for settlement in the southern rock lobster, *Jasus edwardsii*. *Marine Biology.*

Hinojosa IA, Green BS, Gardner C, Hesse J, Stanley J & A. Jeffs. *In review.* Reef sound as an orientation cue for shoreward migration by pueruli of the southern rock lobster, *Jasus edwardsii. PloS ONE.*

Stanley JA, Hesse J, **Hinojosa** IA & AG Jeffs. 2015. Inducers of settlement and moulting in post‐larval spiny lobster. *Oecologia* 178: 685-697.

Hinojosa IA, Green BS, Gardner C, & A Jeffs. 2015. Settlement and early survival of southern rock lobster, *Jasus edwardsii*, under climate-driven decline of kelp habitats. *ICES Journal of Marine Science* 72(Supplement 1): i59-i68.

7.2 Other publications generated during thesis studies, but not directly related.

Thiel M, **Hinojosa** IA, Miranda L, Pantoja J, Rivadeneira MM, & N. Vásquez. 2013. Anthropogenic marine debris in the coastal enviroment: a multi-year comparison between coastal waters and local beaches. *Marine Pollution Bulletin* 71: 307-316.

Wichmann C-S, **Hinojosa** IA & M Thiel. 2012. Floating kelps in Patagonian Fjords: an important vehicle for rafting invertebrates and its relevance for biogeography. *Marine Biology* 159:2035-2049.

Espinoza-Fuenzalida NL, Acuña E, **Hinojosa** IA & M Thiel. 2012. Reproductive biology of two species of squat lobsters - Female receptivity and interbrood intervals. *Journal of Crustacean Biology* 32:565-574.

Gutow L, Long JD, Cerda O, **Hinojosa** IA, Rothäusler E, Tala F & M Thiel. 2012. Herbivorous amphipods inhabit protective microhabitats within sporophytes of giant kelp *Macrocystis pyrifera. Marine Biology* 159:141–149.

Rothäusler E, Gómez I, **Hinojosa** IA, Karsten U, Miranda L, Tala F & M Thiel. 2011. Kelp rafts in the Humboldt Current: Interplay of abiotic and biotic factors limit their floating persistence and dispersal potential. *Limnology & Oceanography* 56: 1751–1763.

Thiel M, **Hinojosa** IA, Joschko T & L Gutow. 2011. Spatio-temporal distribution of floating objects in the German Bight (North Sea). *Journal of Sea Research* 65:368-379.

Rothäusler E, Gómez I, **Hinojosa** IA, Karsten U, Tala F & M Thiel. 2011. Physiological performance of floating giant kelp *Macrocystis pyrifera* (Phaeophyceae): latitudinal variability in the effects of temperature and grazing. *Journal of Phycology* 47:269-281.

Hinojosa IA, Rivadeneira MM & M Thiel. 2011. Temporal and spatial distribution of floating objects in coastal waters of central-southern Chile and Patagonian fjords. *Continental Shelf Research.* 31: 172-186.

Supporting information Chapter 2

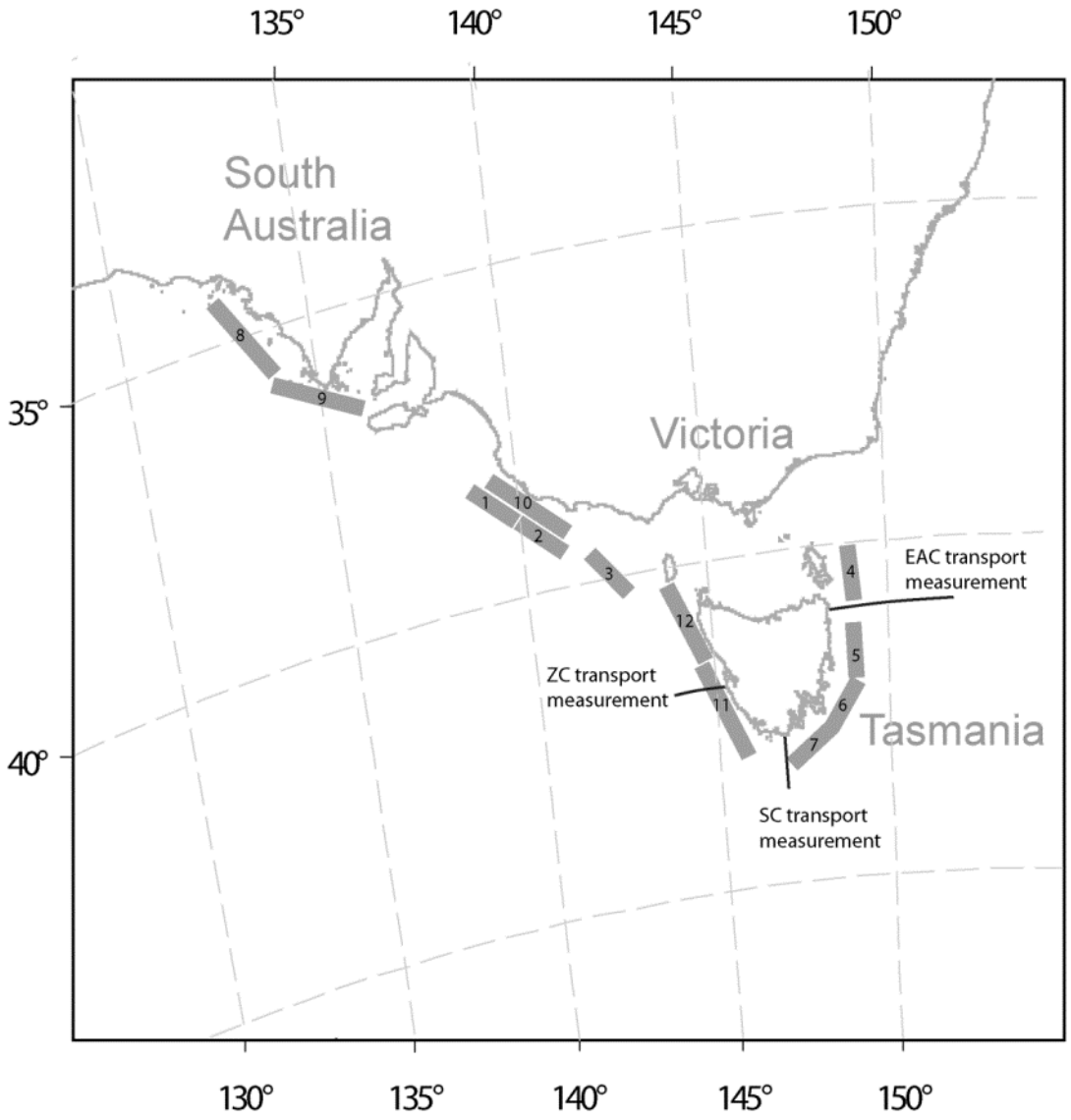


Figure S1. Blocks used to extract monthly data for waves (height and period), winds (strength, u and v components) and sea surface temperature from February 1997 to July 2010. Blocks are numbered 1 to 12 and run approximately parallel to the coast. Blocks 1 to 7 are in offshore areas and 8 to 12 are inshore (on-shelf) areas. Black lines on the map represent the sections where the current transport from East Australian Current extension (EAC), Zeehan Current (ZC) and the flow off the southern tip of Tasmania (South Cape, SC) were calculated from 1994 to 2011 (EAC = 148.3°E to 151°E along 41°S; ZC = 144.7°E to 145.2°E along 42.5°S; SC = 44.2°S to 43.6°S along 146.8°E). Positive values in EAC and ZC represented northward flow and Positive represented eastward flow in SC.

Table 1S. Codes used in dynamic regression modelling.

Code for lag on months	Meaning	Example
$L1	1 (month lagged)	
$L2	2(months lagged)	tasbiL$L2: puerulus settle at Bicheno 2 months ago
...	...	
$L12	12(months lagged)	

Code for settlement sites	Meaning	Example
sabpL	Beachport (A)	
salivL	Livingston Bay (B)	
sabfL	Blackfellows Caves (C)	sabfL$L2: puerulus settle at Blackfellows Caves 2 months ago
vicpcL	Port Campbell (D)	
tasmoL	Recherche bay (E)(or Mouldies)	
tasipL	South Arm (F)(Iron Pot)	
tasbiL	Bicheno (G)	

Sea surface temperature code	Block on map	Example
b1tL	1	
b2tL	2	b5tL$L4: SST in block 5 four months ago
…	…	
b12tL	12	

Code for wind and wave	Meaning	Example
wvhL	Wave height	
wvpL	Wave period	b9wvpL$L1: waves period in block 9 one month ago
wdL	Wind strength	
wduL	Wind u component	
wdvL	Wind v component	

Code for current transport	Meaning	Example
EAC_min	EAC Maximum Southward transport	
EAC_max	EAC Maximum Northward transport	
EAC_mean	EAC Monthly average transport	
EAC_delta	EAC Monthly variability transport	EAC_max$L4: East Australian Current northward transport four month ago
ZC_min	ZC Maximum Southward transport	
ZC_max	ZC Maximum Northward transport	
ZC_mean	ZC Monthly average transport	
ZC_delta	ZC Monthly variability transport	
SC_min	SC Maximum Southward transport	
SC_max	SC Maximum Northward transport	
SC_mean	SC Monthly average transport	
SC_delta	SC Monthly variability transport	

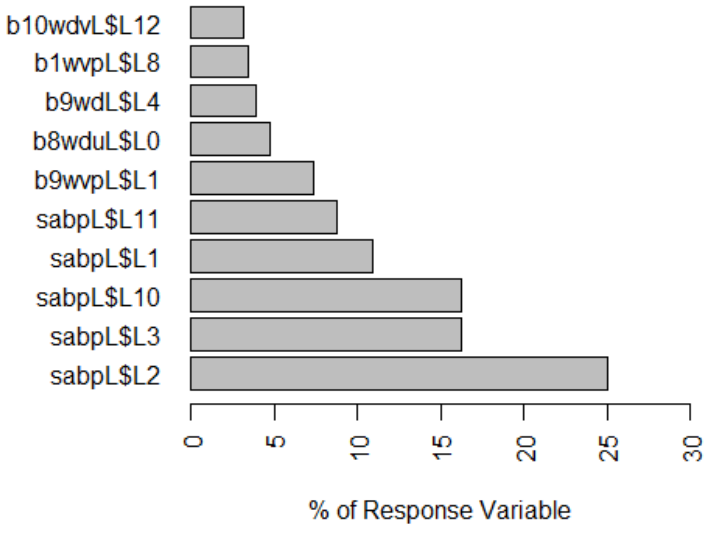
Table 2S. Dynamic regression modelling (DRM) of settlement data for **Beachport (A)**, South Australia.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.0004569	0.0055940	0.082	0.935029
sabpL$L1	-0.5459245	0.0672862	-8.113	2.33e-13 ***
sabpL$L2	-0.4703054	0.0649318	-7.243	2.74e-11 ***
sabpL$L10	-0.3342165	0.0595503	-5.612	1.04e-07 ***
b9wvpL$L1	0.0832581	0.0252432	3.298	0.001236 **
sabpL$L3	-0.3970292	0.0645090	-6.155	7.58e-09 ***
b10wdvL$L12	0.0071538	0.0028649	2.497	0.013690 *
b8wduL$L0	0.0248053	0.0073747	3.364	0.000994 ***
b1wvpL$L8	0.0226593	0.0121919	1.859	0.065205
sabpL$L11	-0.2447865	0.0644151	-3.800	0.000216 ***
b9wdL$L4	-0.0367710	0.0138275	-2.659	0.008750 **

Residual standard error: 0.0685 on 139 degrees of freedom

Multiple R-squared: 0.5657, Adjusted R-squared: 0.5344

F-statistic: 18.1 on 10 and 139 DF, p-value: < 2.2e-16



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test to
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value	Lag (months)	p-value
1	0.194756	13	0.147272
2	0.430479	14	0.189753
3	0.393621	15	0.169688
4	0.518636	16	0.164500
5	0.447540	17	0.184294
6	0.345735	18	0.234283
7	0.423378	19	0.261791
8	0.258757	20	0.269312
9	0.341035	21	0.218761
10	0.292073	22	0.210543
11	0.373774	23	0.254574
12	0.106623	24	0.026285

Variance Inflation factor. VIF values should ideally be lower than 5.0

Variable	VIF
sabpL$L1	1.453010
sabpL$L2	1.352085
sabpL$L10	1.107425
b9wvpL$L1	1.200704
sabpL$L3	1.338960
b10wdvL$L12	1.039446
b8wduL$L0	1.038045
b1wvpL$L8	1.130652
sabpL$L11	1.266832
b9wdL$L4	1.142012

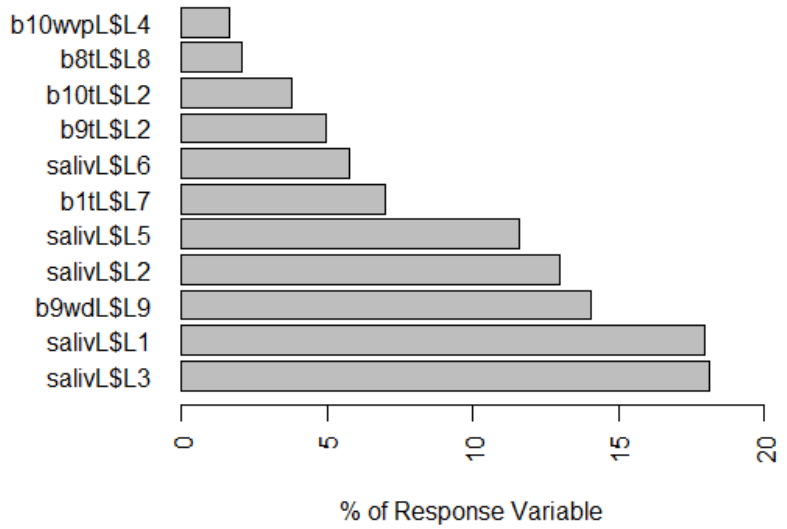
Table 3S. Dynamic regression modelling (DRM) of settlement data for **Livingston Bay (B)**, South Australia.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.002425	0.006329	0.383	0.702195
salivL$L1	-0.504823	0.068879	-7.329	1.77e-11 ***
salivL$L2	-0.352921	0.072077	-4.896	2.69e-06 ***
salivL$L3	-0.241295	0.071473	-3.376	0.000956 ***
b1tL$L7	0.121728	0.040344	3.017	0.003038 **
b8tL$L8	0.099933	0.033646	2.970	0.003512 **
b10wvpL$L4	0.012793	0.005904	2.167	0.031959 *
salivL$L6	0.293624	0.068754	4.271	3.61e-05 ***
salivL$L5	0.368797	0.071649	5.147	8.91e-07 ***
b10tL$L2	-0.127357	0.034653	-3.675	0.000339 ***
b9tL$L2	0.159678	0.053484	2.985	0.003350 **
b9wdL$L9	-0.067203	0.015880	-4.232	4.20e-05 ***

Residual standard error: 0.07744 on 138 degrees of freedom

Multiple R-squared: 0.4802, Adjusted R-squared: 0.4387

F-statistic: 11.59 on 11 and 138 DF, p-value: 4.209e-15



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value	Lag (months)	p-value
1	0.147302	13	0.407289
2	0.235236	14	0.113412
3	0.409916	15	0.063170
4	0.489092	16	0.086656
5	0.395665	17	0.117907
6	0.266286	18	0.150763
7	0.271185	19	0.173990
8	0.285293	20	0.043848
9	0.288689	21	0.042959
10	0.232798	22	0.057600
11	0.272737	23	0.072674
12	0.327685	24	0.092856

Variance Inflation factor. VIF values
should ideally be lower than 5.0

Variable	VIF
salivL$L1	1.260412
salivL$L2	1.379071
salivL$L3	1.347717
b1tL$L7	1.150882
b8tL$L8	1.168170
b10wvpL$L4	1.136427
salivL$L6	1.269863
salivL$L5	1.371312
b10tL$L2	1.823121
b9tL$L2	1.765426
b9wdL$L9	1.189325

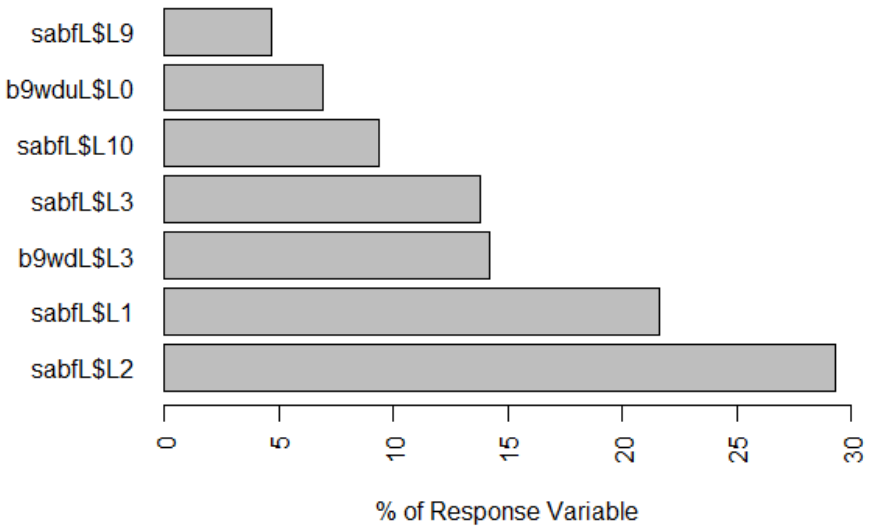
Table 4S. Dynamic regression modelling (DRM) of settlement data for **Blackfellows Caves (C)**, South Australia.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.003398	0.009600	0.354	0.723933
sabfL$L1	-0.504791	0.075803	-6.659	5.59e-10 ***
sabfL$L2	-0.566154	0.076140	-7.436	8.99e-12 ***
sabfL$L3	-0.276590	0.073779	-3.749	0.000258 ***
b9wdL$L3	-0.073900	0.023023	-3.210	0.001642 **
b9wduL$L0	0.032949	0.010485	3.143	0.002039 **
sabfL$L10	-0.249441	0.068548	-3.639	0.000382 ***
sabfL$L9	-0.148961	0.067387	-2.211	0.028669 *

Residual standard error: 0.1175 on 142 degrees of freedom

Multiple R-squared: 0.4239, Adjusted R-squared: 0.3955

F-statistic: 14.93 on 7 and 142 DF, p-value: 1.64e-14



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value	Lag (months)	p-value
1	0.284281	13	0.000622
2	0.288955	14	0.000132
3	0.479643	15	0.000248
4	0.603446	16	0.000417
5	0.610592	17	0.000557
6	0.049988	18	0.000976
7	0.083519	19	0.000754
8	0.098122	20	0.001173
9	0.040216	21	0.001347
10	0.009828	22	0.002127
11	0.000359	23	0.002625
12	0.000344	24	0.003605

Variance Inflation factor. VIF values should ideally be lower than 5.0

Variable	VIF
sabfL$L1	1.411233
sabfL$L2	1.416333
sabfL$L3	1.325753
b9wdL$L3	1.08381
b9wduL$L0	1.263255
sabfL$L10	1.193157
sabfL$L9	1.155126

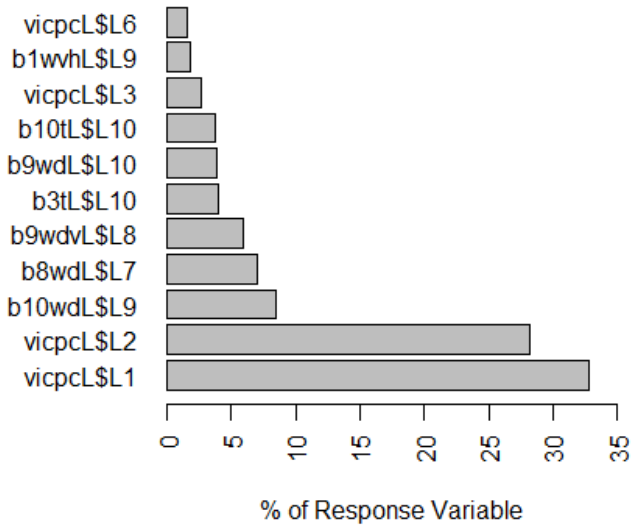
Table 5S. Dynamic regression modelling (DRM) of settlement data for **Port Campbell (D)**,Victoria.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.010025	0.007041	-1.424	0.15677
vicpcL$L1	-0.771645	0.070459	-10.952	< 2e-16 ***
vicpcL$L2	-0.575888	0.082892	-6.947	1.34e-10 ***
b10wdL$L9	-0.086028	0.034649	-2.483	0.01423 *
b8wdL$L7	0.093648	0.034927	2.681	0.00823 **
b3tL$L10	-0.144962	0.053076	-2.731	0.00713 **
b9wdvL$L8	0.008843	0.002843	3.110	0.00227 **
b10tL$L10	0.055364	0.032895	1.683	0.09463
b9wdL$L10	-0.050632	0.017751	-2.852	0.00501 **
vicpcL$L3	-0.221986	0.072343	-3.069	0.00259 **
vicpcL$L6	0.113554	0.056552	2.008	0.04660 *
b1wvhL$L9	0.114836	0.055728	2.061	0.04122 *

Residual standard error: 0.0857 on 138 degrees of freedom

Multiple R-squared: 0.6351, Adjusted R-squared: 0.606

F-statistic: 21.84 on 11 and 138 DF, p-value: < 2.2e-16



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value	Lag (months)	p-value
1	0.126396	13	0.350885
2	0.113713	14	0.007815
3	0.147628	15	0.009051
4	0.161487	16	0.013096
5	0.257497	17	0.019927
6	0.221832	18	0.029226
7	0.247531	19	0.040883
8	0.305198	20	0.056375
9	0.295095	21	0.050186
10	0.374831	22	0.067999
11	0.462641	23	0.020490
12	0.446932	24	0.028775

Variance Inflation factor. VIF values should ideally be lower than 5.0

Variable	VIF
vicpcL$L1	1.877451
vicpcL$L2	2.501777
b10wdL$L9	1.327278
b8wdL$L7	1.114588
b3tL$L10	1.461943
b9wdvL$L8	1.102569
b10tL$L10	1.476194
b9wdL$L10	1.191304
vicpcL$L3	1.884202
vicpcL$L6	1.070431
b1wvhL$L9	1.34392

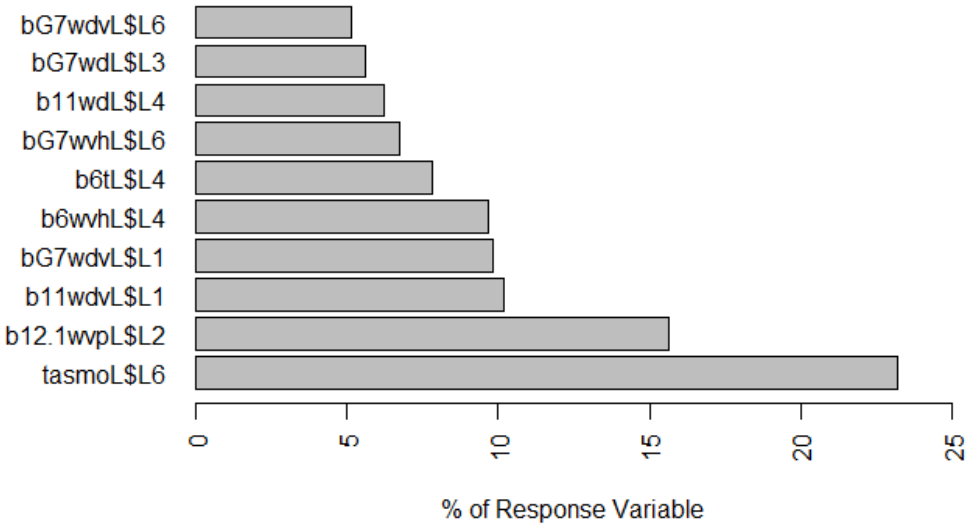
Table 6S. Dynamic regression modelling (DRM) of settlement data for **Recherche Bay (E)**,Tasmania.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.003995	0.007232	-0.552	0.581560
tasmoL$L6	0.123729	0.028647	4.319	2.96e-05 ***
b12.1wvpL$L2	0.219531	0.065771	3.338	0.001084 **
bG7wdvL$L1	-0.042118	0.012601	-3.342	0.001067 **
bG7wvhL$L6	0.312889	0.087112	3.592	0.000455 ***
b6wvhL$L4	0.105685	0.045864	2.304	0.022686 *
b11wdvL$L1	0.016583	0.005685	2.917	0.004121 **
bG7wdvL$L6	0.020410	0.009433	2.164	0.032199 *
b11wdL$L4	-0.065636	0.030464	-2.155	0.032921 *
bG7wdL$L3	-0.031137	0.013283	-2.344	0.020488 *
b6tL$L4	-0.100333	0.045299	-2.215	0.028395 *

Residual standard error: 0.0885 on 139 degrees of freedom

Multiple R-squared: 0.3111, Adjusted R-squared: 0.2616

F-statistic: 6.278 on 10 and 139 DF, p-value: 6.714e-08



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value	Lag (months)	p-value
1	3.31E-07	13	4.12E-08
2	7.66E-10	14	8.86E-08
3	3.14E-11	15	1.51E-07
4	6.43E-12	16	3.48E-07
5	2.33E-11	17	7.47E-07
6	5.51E-11	18	1.52E-06
7	1.81E-10	19	3.15E-06
8	6.17E-10	20	2.93E-06
9	1.86E-09	21	3.85E-06
10	5.49E-09	22	7.00E-06
11	1.41E-08	23	1.33E-05
12	3.61E-08	24	2.13E-05

Variance Inflation factor. VIF values
should ideally be lower than 5.0

Variable	VIF
tasmoL$L6	1.048464
b12.1wvpL$L2	1.017699
bG7wdvL$L1	1.853396
bG7wvhL$L6	1.207141
b6wvhL$L4	1.165646
b11wdvL$L1	1.970366
bG7wdvL$L6	1.09859
b11wdL$L4	1.0992
bG7wdL$L3	1.090839
b6tL$L4	1.153285

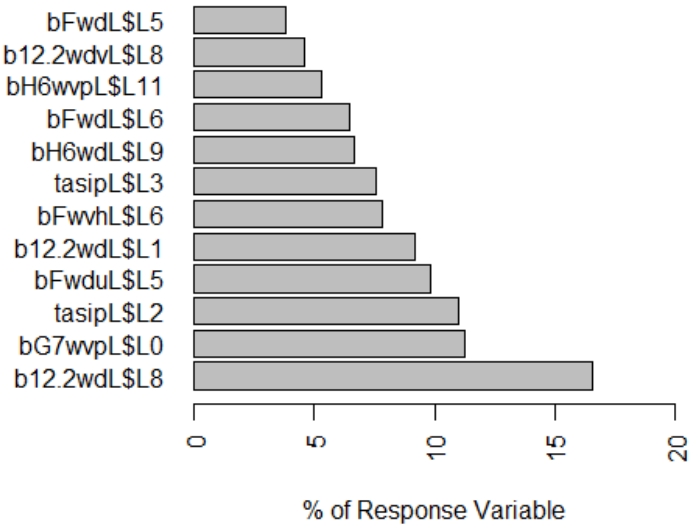
Table 7S. Dynamic regression modelling (DRM) of settlement data for **South Arm (F)**,Tasmania.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.00323	0.01756	-0.184	0.854139
b12.2wdL$L8	-0.57391	0.223608	-2.567	1.13E-02***
bFwdL$L6	-0.10165	0.024703	-4.115	6.65E-05***
bFwvhL$L6	0.546587	0.185678	2.944	3.81E-03***
bG7wvpL$L0	1.734789	0.527946	3.286	0.001291**
b12.2wdvL$L8	-0.03689	0.012685	-2.908	0.004244**
bH6wvpL$L11	-0.97932	0.311329	-3.146	0.002033**
bH6wdL$L9	0.14628	0.067359	2.172	0.031604*
bFwduL$L5	-0.0511	0.012428	-4.112	6.73E-05***
bFwdL$L5	0.076267	0.025372	3.006	0.00315**
b12.2wdL$L1	-0.62268	0.210769	-2.954	0.00369**
tasipL$L3	-0.31994	0.081285	-3.936	0.000131***
tasipL$L2	-0.26797	0.081859	-3.274	0.001344**

Residual standard error: 0.215 on 137 degrees of freedom

Multiple R-squared: 0.416, Adjusted R-squared: 0.3649

F-statistic: 8.133 on 12 and 137 DF, p-value: 2.14e-11



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value	Lag (months)	p-value
1	4.08E-05	13	6.63E-07
2	4.33E-09	14	1.39E-06
3	4.48E-09	15	3.06E-06
4	3.05E-09	16	6.49E-06
5	1.42E-09	17	1.34E-05
6	2.70E-09	18	2.33E-05
7	8.46E-09	19	2.38E-05
8	2.06E-08	20	4.52E-05
9	5.17E-08	21	8.37E-05
10	7.21E-08	22	1.15E-04
11	1.81E-07	23	9.74E-05
12	2.79E-07	24	1.72E-04

Variance Inflation factor. VIF values
should ideally be lower than 5.0

Variable	VIF
b12.2wdL$L8	1.245159
bFwdL$L6	3.283583
bFwvhL$L6	3.022733
bG7wvpL$L0	1.061342
b12.2wdvL$L8	1.164042
bH6wvpL$L11	1.195892
bH6wdL$L9	1.117483
bFwduL$L5	3.511327
bFwdL$L5	3.486768
b12.2wdL$L1	1.076759
tasipL$L3	1.411712
tasipL$L2	1.418825

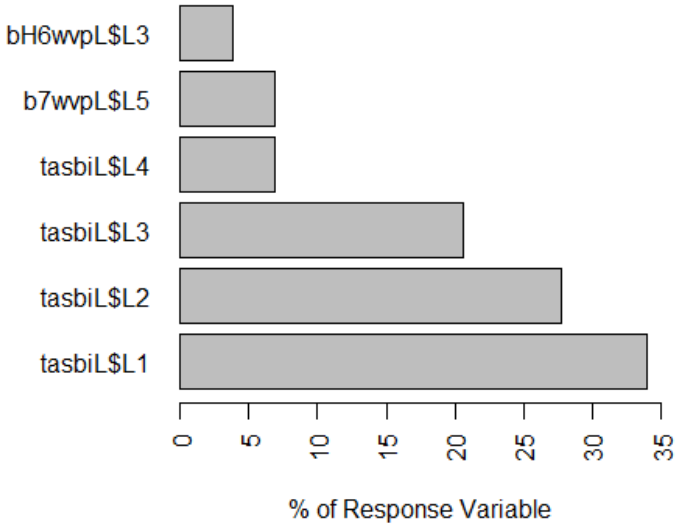
Table 8S. Dynamic regression modelling (DRM) of settlement data for **Bicheno (G)**,Tasmania.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.00045	0.014433	-0.031	0.97527
tasbiL$L1	-0.87328	0.076547	-11.408	<2E-16***
tasbiL$L2	-0.81785	0.092178	-8.872	2.66E-15***
tasbiL$L3	-0.57991	0.091235	-6.356	2.60E-09***
b7wvpL$L5	4.915379	1.778361	2.764	0.00646**
tasbiL$L4	-0.25196	0.075155	-3.353	0.00102**
bH6wvpL$L3	-0.61389	0.243837	-2.518	0.01292*

Residual standard error: 0.1768 on 143 degrees of freedom

Multiple R-squared: 0.535, Adjusted R-squared: 0.5155

F-statistic: 27.42 on 6 and 143 DF, p-value: < 2.2e-16



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value	Lag (months)	p-value
1	0.826161	13	0.37553111
2	0.647754	14	0.45231496
3	0.808816	15	0.50003672
4	0.689821	16	0.31468028
5	0.331266	17	0.3506132
6	0.076934	18	0.38758496
7	0.077665	19	0.26572453
8	0.121382	20	0.32400868
9	0.13119	21	0.32464131
10	0.184614	22	0.36314729
11	0.236815	23	0.4092354
12	0.303389	24	0.46777529

Variance Inflation factor. VIF values
should ideally be lower than 5.0

Variable	VIF
tasbiL$L1	1.802328
tasbiL$L2	2.662153
tasbiL$L3	2.631648
b7wvpL$L5	1.045834
tasbiL$L4	1.797879
bH6wvpL$L3	1.030519

Bellow the analysis on Tasmanian sites considering the current transport (ZC = Zeehan Current; EAC =East Australian Current & SC = South Cape transport). min = maximum southward transport for EAC and ZC and Westward for SC; max = minimum southward transport or reverse for EAC and ZC; and Eastward for SC; delta = difference in magnitude between min and max value.

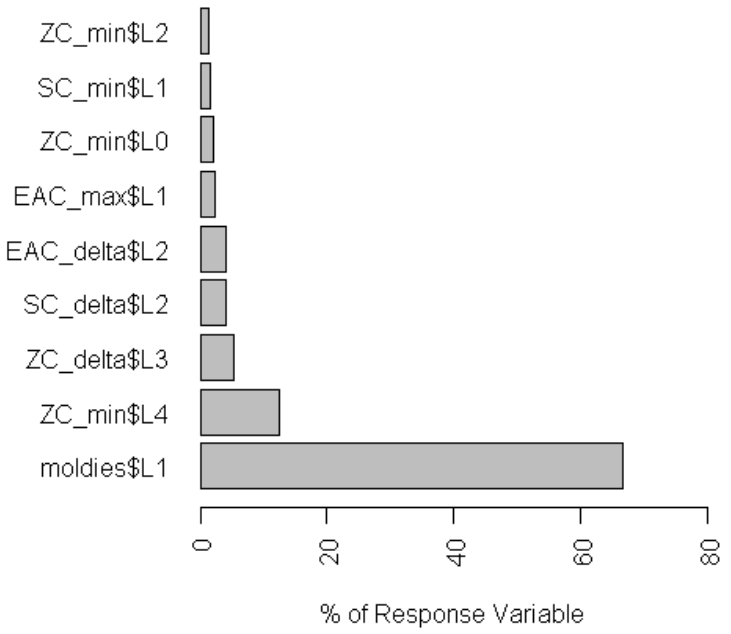
Table 9S. Dynamic regression modelling (DRM) on settlement data of **Recherche Bay (E)**, Tasmania using the current transport lagged 5 months.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	1.631077	0.444774	3.667	0.000307***
moldies$L1	0.409156	0.059475	6.879	6.10E-11***
ZC_min$L4	0.266757	0.111058	2.402	0.017134*
ZC_delta$L3	-0.289147	0.120656	-2.396	0.017387*
EAC_delta$L2	-0.019062	0.007929	-2.404	0.017041*
SC_delta$L2	0.442749	0.216729	2.043	0.042252*
EAC_max$L1	-0.012262	0.006412	-1.912	0.057106
ZC_min$L0	-0.20088	0.114797	-1.75	0.081529
ZC_min$L2	0.204692	0.128409	1.594	0.112352
SC_min$L1	0.402636	0.265539	1.516	0.130874

Residual standard error: 1.089 on 221 degrees of freedom

Multiple R-squared: 0.383, Adjusted R-squared: 0.3579

F-statistic: 15.24 on 9 and 221 DF, p-value: < 2.2e-16



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value
1	0.4364659
2	0.3121134
3	0.1150004
4	0.1891845
5	0.1283988

Variance Inflation factor. VIF values
should ideally be lower than 5.0

Variable	VIF
moldies$L1	1.267023
ZC_min$L4	1.275487
ZC_delta$L3	1.271946
EAC_delta$L2	1.05843
SC_delta$L2	1.299082
EAC_max$L1	1.036578
ZC_min$L0	1.370264
ZC_min$L2	1.706242
SC_min$L1	1.10091

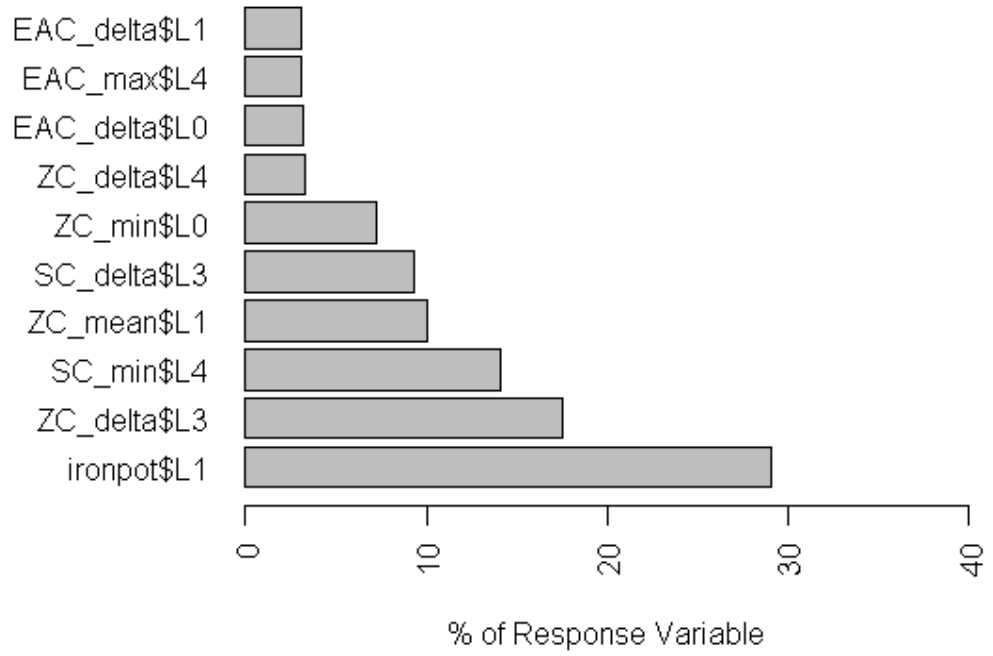
Table 10S. Dynamic regression modelling (DRM) on settlement data of **South Arm (F)**, Tasmania using the current transport lagged 5 months.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	1.95137	1.13583	1.718	0.087199
ironpot$L1	0.25673	0.0597	4.3	2.57E-05***
SC_min$L4	2.1727	0.62064	3.501	0.000562***
ZC_mean$L1	1.17883	0.3965	2.973	0.003276**
SC_delta$L3	2.08341	0.52674	3.955	0.000103***
ZC_delta$L3	-0.74086	0.31589	-2.345	0.019900*
ZC_min$L0	-0.53851	0.27845	-1.934	0.054404
ZC_delta$L4	-0.51393	0.28072	-1.831	0.068484
EAC_max$L4	0.02537	0.01557	1.629	0.104828
EAC_delta$L1	-0.03699	0.01981	-1.867	0.063163
EAC_delta$L0	0.03064	0.01971	1.555	0.121491

Residual standard error: 2.624 on 220 degrees of freedom

Multiple R-squared: 0.2576, Adjusted R-squared: 0.2238

F-statistic: 7.633 on 10 and 220 DF, p-value: 1.932e-10



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value
1	0.9846285
2	0.6234746
3	0.8040406
4	0.7643857
5	0.8287678

Variance Inflation factor. VIF values
should ideally be lower than 5.0

Variable	VIF
ironpot$L1	1.061547
SC_min$L4	1.046068
ZC_mean$L1	1.392155
SC_delta$L3	1.316864
ZC_delta$L3	1.501228
ZC_min$L0	1.38819
ZC_delta$L4	1.181133
EAC_max$L4	1.045445
EAC_delta$L1	1.139427
EAC_delta$L0	1.108733

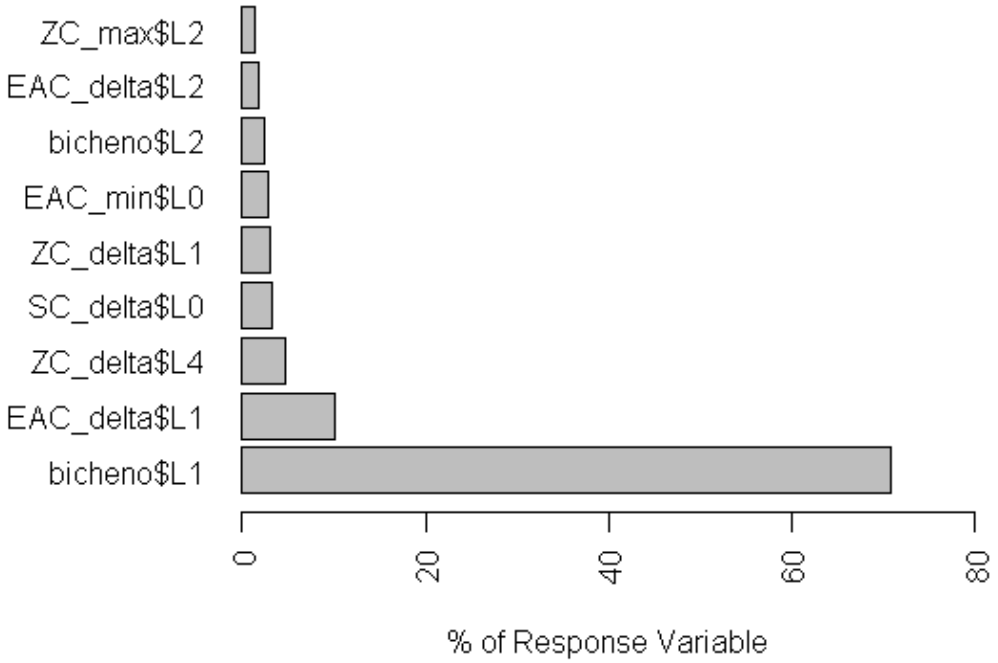
Table 11S. Dynamic regression modelling (DRM) of settlement data for **Bicheno (G)**, Tasmania using the current transport lagged 5 months.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	4.61459	1.3524	3.412	0.000766***
bicheno$L1	0.42783	0.06389	6.696	1.75E-10***
EAC_delta$L1	-0.07569	0.02192	-3.453	0.000665***
ZC_delta$L4	-0.62561	0.29685	-2.108	0.036200*
ZC_delta$L1	-0.83998	0.29874	-2.812	0.005371**
SC_delta$L0	1.12431	0.52577	2.138	0.033581*
EAC_min$L0	-0.03147	0.01655	-1.902	0.058517
bicheno$L2	0.12829	0.06217	2.063	0.040238*
EAC_delta$L2	-0.03471	0.02251	-1.542	0.124589
ZC_max$L2	0.48275	0.3409	1.416	0.158147

Residual standard error: 2.932 on 221 degrees of freedom

Multiple R-squared: 0.4078, Adjusted R-squared: 0.3837

F-statistic: 16.91 on 9 and 221 DF, p-value: < 2.2e-16



Model validation with the Breusch & Godfrey test to assess the presence of serial autocorrelation and the Variance inflation factor to assess multicollinearity.

Breusch & Godfrey test
(H_0: $\rho_1 = \rho_2 = \rho_2 = \cdots = \rho_p = 0$)

Lag (months)	p-value
1	0.8233654
2	0.9596888
3	0.5975623
4	0.1901135
5	0.2898537

Variance Inflation factor. VIF values
should ideally be lower than 5.0

Variable	VIF
bicheno$L1	1.520595
EAC_delta$L1	1.118085
ZC_delta$L4	1.058132
ZC_delta$L1	1.07639
SC_delta$L0	1.049426
EAC_min$L0	1.123501
bicheno$L2	1.436357
EAC_delta$L2	1.177143
ZC_max$L2	1.07348

Supporting information Chapter 5

Supplementary material is available at *ICESJMS* online version of the paper and contains: S1, a video of the behavioural response of the early benthic phase of the southern rock lobster when it was stalked by the Cardinal fish (*Vincentia* sp.) and by the Speedy crab (*Plagusia chabrus*). S2, a photo of the yellow-saddled wrasse (*Notolabrus fucicola*) with the monofilament tether line and swivel in their mouth.

S2, a photograph of the yellow-saddled wrasse (*Notolabrus fucicola*) with the monofilament tether line and swivel in their mouth.